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EVOLUTION OF FACIAL MUSCULATURE AND CUTANEOUS FIELD OF TRIGEMINUS

PART I

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IN THE following chapters the author presents conclusions from detailed comparative anatomical, embryological and racial anatomical studies (1913–30) on the facialis musculature and on the cutaneous field of the *N. trigeminus*, correlated with data obtained from neuro-physiological investigations.

I. THE EVOLUTION OF THE FACIALIS MUSCULATURE FROM LOWER VERTEBRATES TO MAMMALS, WITH A DISTINCT GROUND PLAN IN THE MONOTREMES AND A COMMON GROUND PLAN FOR THE MARSUPIALS AND PLACENTALS

In order to present a comprehensive picture of the marvelous evolution of the facial musculature I shall briefly view conditions in a few selected types of the "ascending scale of Vertebrates," beginning with the Selachians, where the motor facialis field is represented by a comparatively insignificant muscle territory. While a series of scattered earlier publications by Vetter, Tiesing, Stannius, Adams, Walter, Fischer, Ecker, Gaupp, Wiedersheim, Killian, Fürbringer and others referred to facial musculature of certain representatives of the lower Vertebrates, Ruge's classical monograph (1896) finally outlined the evolution of this muscle field in the main groups of the lower vertebrates up to the reptiles, with an attempt to link these with the monotreme mammals. This work of Ruge's afforded a solid basis for further elaboration of this fascinating chapter of comparative anatomy.

The writer has had opportunity to study representatives of the main groups of Vertebrates, including the fishes, amphibians, reptiles and birds of which only a few were examined, while concentrated efforts were directed towards a systematic investigation of the facial musculature in mammals.

Fishes: In the dogfish we find, connected with the branchial skeleton (fig. 1a) a number of serially arranged muscle sections forming the "constrictor musculature" of the gill arches (fig. 1b). This muscula-

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ture is an intrinsic part of the respiratory apparatus. It effects the alternating constriction and distension of the branchial cavity, regulating at the same time the opening and closing of the spiraculum and the real gill clefts. The different segments of the "*M. constrictor superficialis*" are innervated through the 5th to the 10th cranial nerves. The second segment, the musculature of the 2nd branchial or hyoid arch, is situated between the spiraculum and the 1st real gill cleft. It is innervated by the *N. VII*. This small muscle territory represents the facialis musculature, which though already differentiated into several muscle portions, shows a most primitive arrangement.

With the understanding of this simple ground plan, we have the clue to the understanding of conditions found in the other groups of fishes, where further differentiations have taken place in connection with the transformations in the hyoid arch and the skull, and with the formation of a skeleton-supported operculum (fig. 1c) which covers the individual gill clefts (figs. 1a and b). Amongst the fishes, the bony fishes have reached the highest specialization (fig. 1c).

Amphibians: The perennibranchiate and derotremous amphibians show the most primitive conditions amongst this group. The superficial *M. constrictor arcuum visceralium* (fig. 2a) is here separated into different segments, corresponding to the various visceral (branchial) arches. The facial segment, originally a mere portion of the uniform "*M. constrictor superficialis*," has thus become independent, and moreover has reached a greater expansion cranialwards and caudalwards. It is divided into a superficial and a deep layer which, however, have retained their primitive connection dorsally. The deep layer (fig. 2b) is attached to the hyoid bone, with another portion running to the mandible. The latter forms the functionally important *M. depressor mandibulae*.

Conditions found in the other groups of the amphibians can easily be understood from the ground plan already described. The anurous amphibians show great reduction of the superficial facialis musculature (compare figs. 2c and d), while the deep facialis musculature, especially the *M. depressor mandibulae*, is very well developed (fig. 2c).

Reptiles: From conditions typical of the primitive urodele amphibians, we can also understand the arrangement of facialis musculature in the reptiles. Here we find likewise a superficial and a deep layer which have kept their primitive connection dorsally. The deep layer (figs. 3b and d) shows an arrangement similar to that in the urodeles, but the superficial layer (figs. 3a and c) has gained a wider extension, in connection with the formation of a more definite neck region. Arising from the dorso-lateral fascia and extending, with or without interruption (fig. 3a contrasted with fig. 3c), ventrad to be inserted into the ventral median aponeurosis, it forms a well defined *M. sphincter colli*.

Birds: Having evolved from the reptile stem, this highly modified group shows conditions similar to those in the reptiles. There is likewise present a *sphincter colli*, which in long necked birds may show an enormous extension (fig. 4). In its course it covers the longitudinal trapezius muscle, to which it may be closely adherent.

Mammals: In the phylogeny of the Mammals fundamental changes have taken place, leading to a unique development of this muscle field.

In all mammals the superficial facialis musculature has given up its former connection with the deep facialis musculature, and the common innervation through

branches of the *N. facialis* remains the only indication that the two muscle groups belong together genetically.

The *deep facialis musculature* is in the Monotremes differentiated into the *M. stapedius* and *M. styloideus*, while the *M. detrahens mandibulae*, which occasionally has been included in this group, in reality belongs to the masticatory group (compare Huber, 1925, p. 6).

In the Marsupials and part of the Placentals the deep facialis musculature gave rise to the *M. stapedius* and to the posterior belly of the *M. biventer mandibulae* (fig. 6e), while in the rest of the placentals in addition to these muscles, a *M. stylo-hyoideus* has shed off from the deep facialis muscle mass, and furthermore in some forms a *M. jugulo-hyoideus* (fig. 6f). The morphology of the latter is not yet clear (Huber, 1924–25, p. 369, footnote). The *M. biventer mandibulae*, on the other hand, shows manifold modifications and adaptations, which have been dealt with in a large series of publications by various authors (see Huber, 1924, p. 190, ff.).

After having completely become separated off from the deep facialis musculature, the "primitive *Sphincter colli*" of the promammalian ancestors, gave rise to the *superficial facialis musculature* of the mammals. The monotremes (fig. 5) developed along their own line, on a ground plan which is distinctly different from the common marsupio-placentalian ground plan (fig. 6). The superficial facialis musculature gradually expanded over the whole head and gained extensive connections with the freely movable skin. The formerly rigid mask thus became mobile. Certain muscle portions became connected with the newly formed (in the marsupials and placentals movable) outer ear; others grouped around the eyes, and still others attached themselves to the snout.

The striking difference in the snout musculature of the monotreme and marsupio-placentalian plan is in close relation with fundamental differences in the construction of the snout. In *Echidna*, which in this respect shows the more primitive conditions of the two monotremes, the intermaxillary bones are not only intercalated between the maxillary bones but they surround with their prenasal processes a large part of the cartilaginous skeleton of the nose. Posteriorly these processes join with the nasal bones, with which they form the bony roof of the nose (compare fig. 22e). The cartilaginous skeleton of the nose in *Echidna* is thus largely enclosed in a bony framework built up by the maxillary, intermaxillary and nasal bones, and the tip of the snout is rigid as in the reptiles. In *Ornithorhynchus*, modifications of the monotreme plan have taken place in connection with the formation of the bill (see chapter V and figs. 22a–d), which is likewise a rigid structure. In the marsupials and placentals on the other hand through reduction of the bony framework (i.e., through the loss of the prenasal process of the intermaxillary bone), the cartilaginous skeleton of the nose became to a large extent free, and the tip of the nose became movable through facial muscles which insert there.

Other muscle portions then muscularized the newly formed *vestibulum oris* with the bordering lips. Thus a large number of more or less distinct superficial facialis muscles were formed.

It is to be expected that all these individual muscles are innervated by branches of the *N. facialis*, the nerve of the "primitive *Sphincter colli*," which muscle, contrary to the views of Boas and Paulli (see Huber, 1922–23, p. 92–93), is the matrix of the entire superficial facialis musculature. Such an innervation of the superficial facialis musculature exclusively through the *N. facialis* has been doubted by

a series of authors who claimed an additional nerve supply to some of the superficial facialis muscles, by branches from the cervical plexus and *N. trigeminus*. But these doubts were eventually disproven on an experimental basis (Michelsson, 1922; Huber, 1924; Huber and Hughson, 1926).

Embryological development gives further evidence that the superficial facialis musculature is the genetically uniform field of the *N. facialis*. Though our knowledge of the embryology of the field is still very incomplete, a valuable start has been made through the investigations of K. Rabl (1887), G. Killian ('90), J. Popowsky ('95), H. Baum and R. Dobers (1905), H. Rouvière ('06), R. Futamura ('06, '07), W. H. Lewis ('10), F. H. Edgeworth ('14, '23), M. Zuckermann-Zicha ('25), Huber (chapter 7), and others. Through these contributions we learn that in mammals the facialis muscle field starts its development from a small muscle anlage, connected with the hyoid arch. From this primitive anlage split off the deep and the superficial facialis musculature. The latter then leaves its originally restricted territory in the neck region and invades the face, where it differentiates into the many more or less distinct individual muscles. Following this differentiation in the muscle field, the *N. facialis* ramifies, and gradually forms the complicated facial plexus. The embryological development of the facialis musculature of the mammals, including man, thus recapitulates important stages of the phylogenetic development.

The *comparative anatomy* and *phylogeny* of the mammalian superficial facialis musculature is far better known than its embryology. Initiated through the monumental pioneer work of G. Ruge (1885, '87) a large series of publications on this subject have appeared by Tataroff (1887), Süssmayr ('88), Popoff ('90), Schulmann ('90/91, '05), Ruge ('95, '11), Popowsky ('88, '93, '97), Bovero (1903), Baum and Kirsten ('04), Boas and Paulli ('08), Virchow ('08, '15, '23, '24, '27), Bluntschli ('09), Eisler ('12), Ückermann ('12), Huber ('18–30), Michelsson ('21), Paugger ('23), Sullivan and Osgood ('21), Lightoller ('25, '28), Schreiber ('28, '29), and many others. Moreover, much detailed knowledge on the human mimetic musculature with its innumerable individual variations (see Testut, 1884; Le Double, '97; Vilhena, 1911; Eisler, '12; *et alii*) has gradually been accumulated in continuation with the studies of the pioneers among the anatomists dating from the Renaissance (Vesalius, Eustachius, Albinus, Santorini, Sömmering, Cruveilhier, Henle, Gegenbaur). But even with this large amount of literature the field is merely outlined.

Through the investigations of Ruge (1895), Schulmann ('05), Boas and Paulli ('08), Huber ('30), and others, it became known that already in the *Monotremes*, in these most archaic, strangely specialized mammals, the superficial facialis musculature is well developed and specialized (compare figs. 5, 13c and d). The monotremes, as already indicated, show features of their own. It is indeed impossible to homologize strictly the various groups of their facial muscles with those of the marsupials and placentals.

While the phylogeny of the superficial facialis musculature of the monotremes is still imperfectly understood we have now, owing to detailed, painstaking studies of various investigators, a fair knowledge of the evolution of this muscle field in the *Marsupials and Placentals*. In several previous publications (Huber, 1918, '22/23, '24; Huber and Hughson, '26) the author has given data upon which his conception of the derivation of the superficial facialis musculature was based.

The author's concept differs in fundamental points from the concept of Ruge (1885, '87), which was until most recent times almost generally accepted. The new concept may here briefly be summed up: From the "primitive *Sphincter colli*" restricted to the neck region as it still is in the modern reptiles and presumably was in the reptilian ancestors of the marsupials and placentals, there have shed off the undifferentiated platysma and *sphincter colli profundus*. These two primary muscle layers invaded the face, where they subsequently differentiated into the more or less distinct facial muscles. The platysma evidently gave rise to the *M. platysma colli et faciei*, and to the postauriculo-occipital muscle group, which includes part of the extrinsic and intrinsic ear muscles (figs. 6a and b). The rest of the superficial facialis musculature was derived from the *sphincter colli profundus* (figs. 6c and d).

According to Ruge's concept, based on his fundamental investigations on primates, the musculature of the cheek walls and lips alone was considered to be derived from the *sphincter colli profundus*, while the rest of the superficial facialis musculature was believed to have arisen from the platysma.

However, through more recent, largely unpublished investigations on representatives of marsupials and a large series of placentals, the author has obtained ample evidence that the *sphincter colli profundus* must have played a far greater rôle as the matrix for the superficial facialis musculature than Ruge had assumed (compare figs. 7—11). This has most recently been demonstrated beyond doubt to conform with conditions found in the primates (Schreiber, 1928; Huber: figures of chapter 7).

The general plan of the superficial facialis musculature in the Marsupials (Boas and Paulli, 1908; Huber, '25, '30, and others) and primitive Placentals is strikingly similar (Huber), no doubt because the marsupials and placentals are closely related groups.

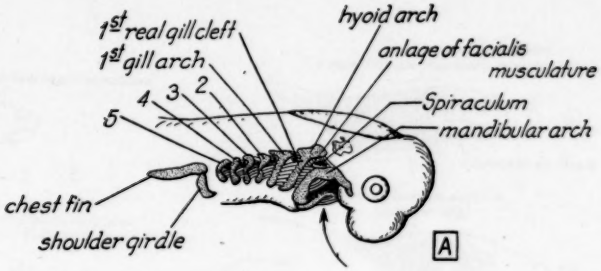
A thorough understanding of the morphology of the superficial facialis musculature of the more primitive placentals enables us to understand conditions found in the higher Placentals (compare chapter 7 on primates). In the various orders of the placentals the superficial facialis musculature has become specialized to different degrees and along many and very different lines. Even when secondarily reduced or in a vestigial stage, it affords material for far reaching evolutionary conclusions. The superficial facial musculature of mammals is also of high systematic value. Although not yet recognized, it has an importance similar to that of the skull, the teeth and the extremities.

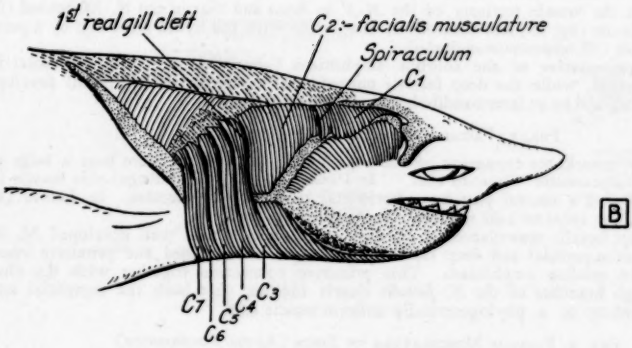
FIG. 1. REPRESENTATIVES OF THE FISHES SHOWING THE INSIGNIFICANT MOTOR FIELD OF THE N. FACIALIS AS PART OF THE BRANCHIAL SKELETON MUSCULATURE

a. Embryo dogfish (modified after Braus). The branchial skeleton is exposed with the serially arranged anlagen of the constrictor musculature of the branchial arches. The section situated between the mandibular and the hyoid arches represents the muscle territory of the *N. facialis*. Note the relation of this muscle segment to the spiraculum in front and to the first real gill cleft behind. The subsequent muscle segments show a similar arrangement.

b. The branchial skeleton musculature of an adult dogfish (after Ruge). C1, connected with the mandibular arch, is the muscle territory of the *N. trigeminus*; C2, the musculature of the hyoid arch (facialis musculature) is bounded in front by the spiraculum, behind by the first real gill cleft; C3 is the muscle field of the *N. IX*; while C4–7 are under the domain of the *N. X*.

c. *Esox lucius*, a representative of the bony fishes (after Vetter), showing the complexity which has developed in the branchial skeleton musculature in connection with the formation of a skeleton supported operculum, which covers the gill clefts. Portions of the facialis musculature are adapted to the opercular skeleton.


1st real gill cleft
1st gill arch
2
3
4
5
hyoid arch
anlage of facialis musculature
Spiraculum
mandibular arch
chest fin
shoulder girdle
A


1st real gill cleft
C2 :- facialis musculature
Spiraculum
C1
B
C7
C5
C6
C4
C3

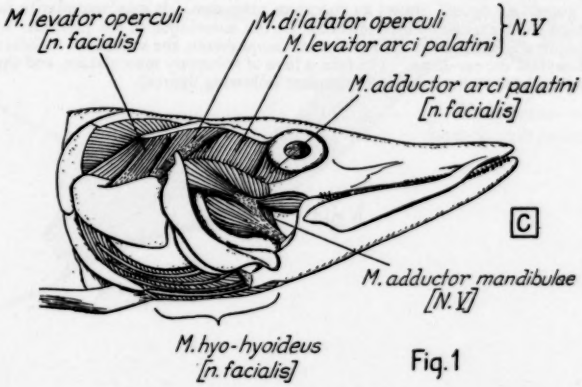

M. levator operculi [n. facialis]
M. dilatator operculi
M. levator arci palatini
N.V
M. adductor arci palatini [n. facialis]
C
M. adductor mandibulae [N.V]
M. hyo-hyoideus [n. facialis]

Fig. 1

FIG. 2. FACIALIS MUSCULATURE IN AMPHIBIANS

a & b. Menopoma, a primitive representative of the urodele amphibians (modified after Ruge). The various sections of the *constrictor arcuum visceralium* have become independent and are further elaborated. C2, the muscle territory of the *N. facialis*, has with its superficial layer expanded cranialwards and caudalwards. It partly covers the muscle territory of the *N. V* in front and that of the *N. IX* behind (fig. a). The deep facialis musculature (fig. 2b) has remained in connection with the hyoid arch, and by a portion is attached to the mandible (*M. depressor mandibulae*).

c & d. Rana as representative of the anurous amphibians (after Gaupp). The superficial facialis musculature has deteriorated, while the deep facialis musculature is represented by a well developed *M. depressor mandibulae* (fig. 2c) and by an intermandibular muscle portion (fig. 2d).

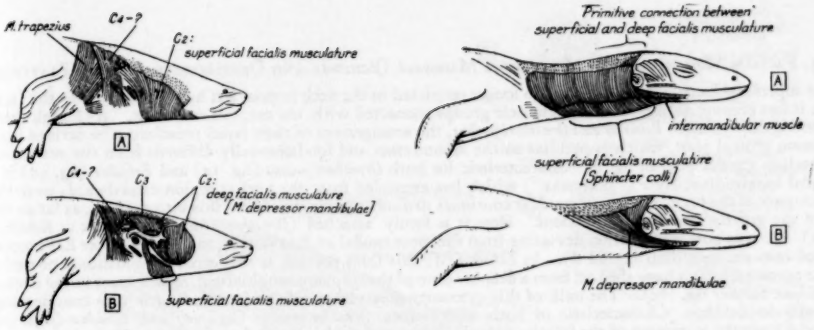
FIG. 3. FACIALIS MUSCULATURE IN REPTILES

The figures show the remarkable expansion of the superficial facialis musculature over a large area of the neck. It forms a characteristic "*Sphincter colli.*" In *Varanus* (fig. 3a, after Ruge) this muscle layer is separated into a dorsal and a ventral part by a horizontal tendinous intersection. In *Lacerta* (fig. 3c, after Huber), however, the *sphincter colli* remains a uniform muscle layer.

b & d show the deep facialis musculature of *Varanus* and *Lacerta* with a well developed *M. depressor mandibulae*. Notice that superficial and deep facialis musculature has retained the primitive connection dorsally just as in the urodele amphibians. This primitive connection together with the characteristic innervation through branches of the *N. facialis* clearly indicate that both the superficial and deep facialis musculature belong to a phylogenetically uniform muscle field.

FIG. 4. FACIALIS MUSCULATURE IN BIRDS (AFTER FÜRBRINGER)

The birds having evolved from the reptile stock show an arrangement of the facialis musculature similar to that of reptiles. The superficial facialis musculature is likewise represented by a *sphincter colli*, which in long necked birds, such as the goose (see figure), shows an enormous extension. It may secondarily fuse with the subjacent *M. trapezius*, which has occasionally been mistaken for the homologue of the platysma of mammals. Noteworthy is the fact that in the birds, as in the reptiles and amphibians, the superficial facialis musculature has not expanded forward beyond the ear-drum. The face is bare of voluntary musculature, and thus remains a rigid mask, this in striking contrast to the mammals (compare following figures).



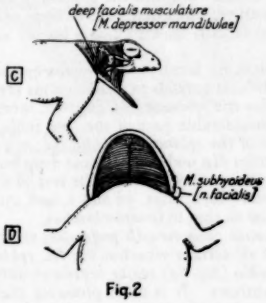


Fig. 2

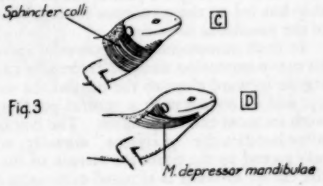


Fig. 3

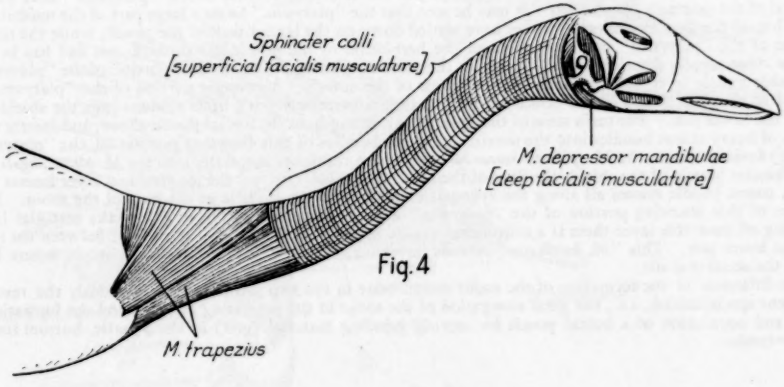


Fig. 4

FIG. 5. FACIALIS MUSCULATURE IN MONOTREME MAMMALS (ECHIDNA AND ORNITHORHYNCHUS SIVE PLATYPUS)

The superficial facialis musculature is no longer restricted to the neck region, but has expanded into the face, where it has become differentiated into muscle groups connected with the ear, eye and snout. Although there are notable differences in *Echidna* and *Ornithorhynchus*, the arrangement of their facial muscles can be derived from a common ground plan, which is peculiar to the monotremes and fundamentally different from the marsupio-placentalian ground plan of fig. 6. Characteristic for both *Ornithorhynchus* (fig. 5a) and *Echidna* (fig. 5d) is a powerful longitudinal layer ("platysma") which has expanded from the nuchal region caudalwards over the anterior part of the back, while oralwards it continues towards the ear and below this into the face, as far as the base of the greatly modified, rigid snout. Here it is firmly attached (*Ornithorhynchus*, figs. 5b & c; *Echidna*, fig. 5e). A very powerful portion deviating from the most caudal section of the longitudinal layer has become inserted into the fore limb (a and d). In *Echidna* (d) this limb portion is reinforced by additional powerful muscle portions, which have shed off from a deep stratum of the common longitudinal muscle mass in the nuchal region (see further fig. 13c). The bulk of this extremity musculature of the facialis field is very considerable, especially in *Echidna*. Characteristic of both monotremes, *Ornithorhynchus* (fig. 5a) and *Echidna* (figs. 5d, 13c and d), are the expansion of the facialis musculature caudalward into the domain of the *panniculus carnosus*, and the interlacing and partial fusion of these two genetically distinct muscle territories. This intimate relationship has led to the erroneous concept that the superficial facialis musculature is merely the forward extension of the *panniculus carnosus*.

In both monotremes the powerful *sphincter colli* is a striking feature. In *Ornithorhynchus* (a) this layer is in its entire expansion situated externally to the "platysma." It extends as a continuous layer from the shoulder region forward close to the base of the snout. In *Echidna* the *sphincter colli* (fig. 5d, more fully shown in figs. 13c and d) covers with a ventral portion (fig. 13d) a considerable part of the fore limb, into which it inserts with its most caudal bundles. The cranial continuation of the *sphincter colli* (fig. 5d, 13c and d) overlaps with some bundles the "platysma" dorsally, while other bundles dip under it. These deep bundles of the *sphincter colli* ascend to the posterior margin of the ear cartilage, where they insert. The rest of the *sphincter colli* from the ear on forward is situated externally to the "platysma" layer (figs. 5d and e, and 13c). It extends as far as the base of the snout, thus showing an extension similar to that in *Ornithorhynchus*.

It is noteworthy that both monotremes lack a continuous *sphincter colli profundus*, which is so characteristic of the marsupio-placentalian ground plan. It is not at all certain whether the *M. sphincter bursae buccalis* of *Ornithorhynchus* (fig. 5c) and the *M. "buccinator"* of *Echidna* (fig. 5e) really represent differentiations of a *pars oris sph. colli profundi*, as has been assumed by former authors. It is more probable that these muscles have arisen from the longitudinal layer at the base of the snout, where this layer inserts into the maxilla with a heavy, coarse bundle mass. Fig. 5b shows in *Ornithorhynchus* the inserting portion of the "platysma" after partial removal of the external *sphincter colli*. It may be seen that the "platysma" forms a large part of the musculature of the buccal pouch. Posteriorly bundles have settled down on the lateral wall of the pouch, while the middle portion of the "platysma" evidently through the herniation of the pouch has thinned out and has in part become subsequently deteriorated. This leaves the most oral section of the middle portion of the "platysma" as a feeble bundle layer, which inserts into the angle of the mouth. A stronger portion of the "platysma" is applied to the wall of the buccal pouch below. It inserts anteriorly with little tendons into the shield-like flap of the lower jaw. The main mass of the "platysma" strengthens the buccal pouch above, and inserts with a mass of heavy coarse bundles into the maxilla. Deeper bundles of this inserting portion of the "platysma" (fig. 5c) deviate to form the *M. sphincter bursae buccalis*, which continues anteriorly into the *M. plicae anguli oris*, the sphincter muscle of the shield-like flaps of the bill. In *Echidna* (fig. 5e) the longitudinal layer inserts with heavy, coarse bundle masses all along the zygomatic arch and to the maxilla at the base of the snout. Deep bundles of this inserting portion of the "platysma" deviate ventralward, forming a weak, vestigial layer. Splitting off from this layer there is a continuous muscle layer ("*M. buccinator*") spread out between the upper and the lower jaw. This "*M. buccinator*" extends forward as far as the tip of the slender snout, where it encircles the small oral slit.

The difference in the formation of the snout musculature in the two monotremes is obviously the result of divergent specialization, i.e., the great elongation of the snout in the ant-eating *Echidna*, and the formation of a bill and acquisition of a buccal pouch for storing grinding material (grit) in the aquatic, bottom feeding *Ornithorhynchus*.

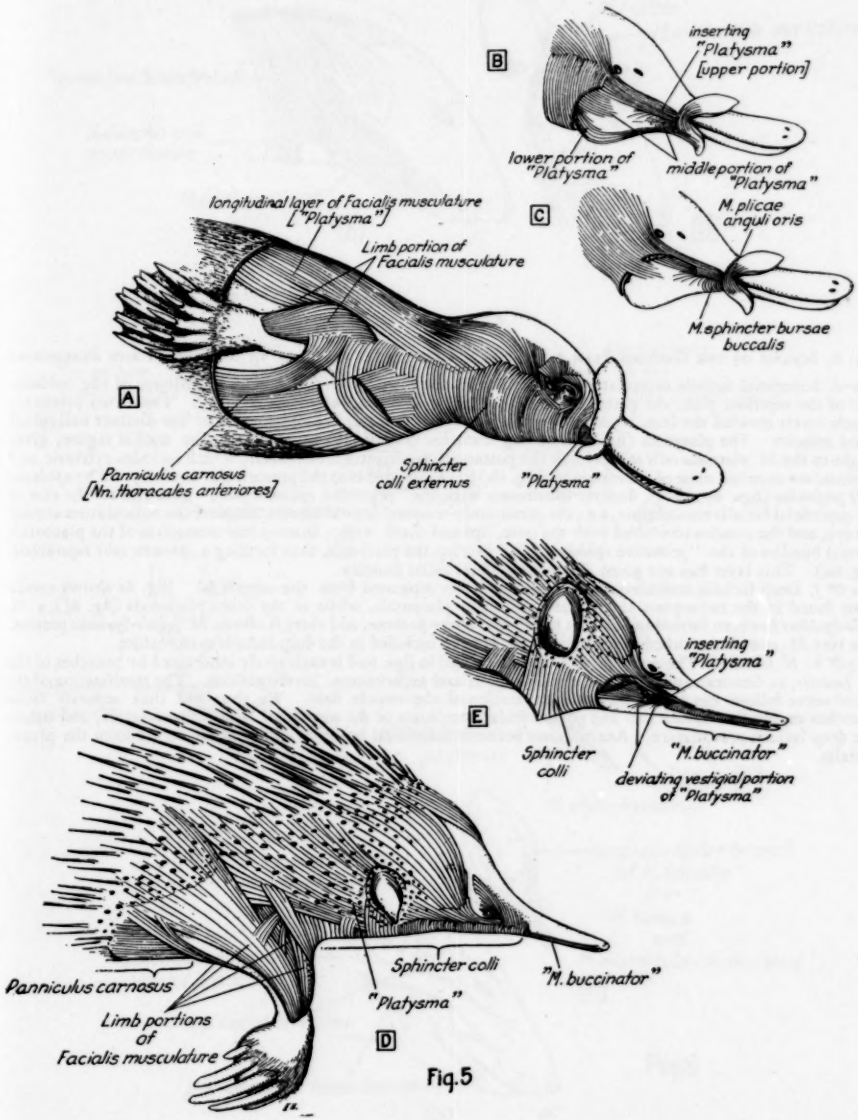

B
inserting "Platysma" [upper portion]
lower portion of "Platysma"
middle portion of "Platysma"
C
M. plicae anguli oris
M. sphincter bursae buccalis
longitudinal layer of Facialis musculature ["Platysma"]
Limb portion of Facialis musculature
A
Panniculus carnosus [Nn. thoracales anteriores]
Sphincter colli externus
"Platysma"
E
inserting "Platysma"
Sphincter colli
"M. buccinator"
deviating vestigial portion of "Platysma"
Panniculus carnosus
Limb portions of Facialis musculature
"Platysma"
Sphincter colli
"M. buccinator"
D

Fig. 5

FIG. 6. SCHEME OF THE GROUND PLAN OF FACIALIS MUSCULATURE COMMON TO MARSUPIALS AND PLACENTALS

a–d. Superficial facialis musculature. From the "primitive *Sphincter colli*," the homologue of the *sphincter colli* of the reptilian plan, the platysma and the *sphincter colli profundus* have shed off. These two primitive muscle layers invaded the face, where they subsequently gave rise to the many, more or less distinct individual facial muscles. The platysma (fig. 6a), arising from the primitive *sphincter colli* in the nuchal region, gives origin to the *M. platysma colli et faciei* and the postauriculo-occipital musculature, which includes extrinsic and intrinsic ear muscles; some of these muscles (fig. 6b) have intruded into the preauricular territory. The *sphincter colli profundus* (figs. 6c and d), directly continuous with the "primitive *sphincter colli*," gave rise to the rest of the superficial facialis musculature, i.e., the preauriculo-temporo-frontal muscle complex, the musculature around the eye, and the muscles connected with the nose, lips and cheek wall. In some representatives of the placentals ventral bundles of the "primitive *sphincter colli*" overlap the platysma, thus forming a *sphincter colli superficialis* (fig. 6a). This layer has not given rise to individual facial muscles.

e & f. Deep facialis musculature, having completely separated from the superficial. Fig. 6e shows conditions found in the marsupials and in some primitive placentals, while in the other placentals (fig. 6f), a *M. stylo-hyoideus* has been formed in addition to the *M. biventer posterior*, and there is often a *M. jugulo-hyoideus* present. The tiny *M. stapedius* enclosed in the middle ear, is to be included in the deep facialis musculature.

g & h. *N. facialis*. The entire muscle field illustrated in figs. 6a-f is exclusively innervated by branches of the *N. facialis*, as demonstrated through morphological and experimental investigations. The ramification of the facial nerve follows the phylogenetic differentiation of the muscle field. We thus find that separate facial branches supply the various pre- and postauricular complexes of the superficial facialis musculature, and others the deep facialis musculature. Anastomoses between individual branches of the facial nerves form the plexus facialis.

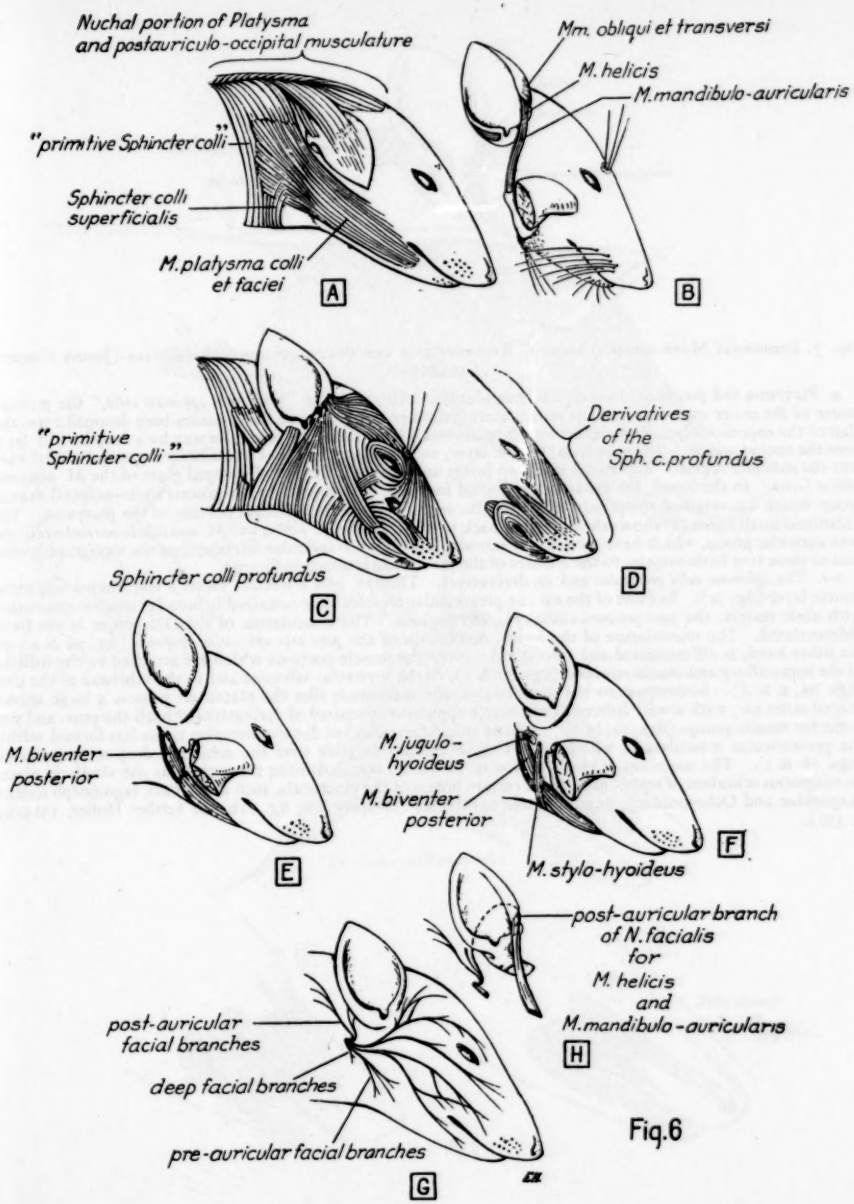

Nuchal portion of Platysma and postauriculo-occipital musculature
"primitive Sphincter colli"
Sphincter colli superficialis
M. platysma colli et faciei
A
Mm. obliqui et transversi
M. helicis
M. mandibulo-auricularis
B
"primitive Sphincter colli"
Sphincter colli profundus
C
Derivatives of the Sph. c. profundus
D
M. biventer posterior
E
M. jugulo-hyoideus
M. biventer posterior
M. stylo-hyoideus
F
post-auricular branch of N. facialis for M. helicis and M. mandibulo-auricularis
H
post-auricular facial branches
deep facial branches
pre-auricular facial branches
G

Fig. 6

FIG. 7. DIDELPHYS MARSUPIALIS (OPOSSUM) REPRESENTING THE POLYPROTODONT MARSUPIALS (JOHNS HOPKINS COLLECTION)

a. Platysma and postauriculo-occipital musculature. Although the "primitive *sphincter colli*," the primary source of the entire superficial facialis musculature (compare fig. 6), has in the opossum been dropped from the plan of the superficial facialis musculature, the platysma still arises in the primitive way by a deep bundle layer from the nuchal region. The superficial bundle layer, on the other hand, has secondarily expanded caudalward into the shoulder region. Superficial and deep layers unite to form the well developed plate of the *M. platysma colli et facici*. In the figure, the ear is shown pulled forward, to demonstrate the postauriculo-occipital muscle group which has retained the primitive connection with its matrix, the nuchal portion of the platysma. The additional small figure (*b*) shows the ear turned back to illustrate the *M. helicis* and *M. mandibulo-auricularis* of the post-auricular group, which have secondarily intruded into the pre-auricular territory (see the topographic relation of these two little muscles to the muscles of the pre-auricular group in fig. 7c).

c–e. The *sphincter colli profundus* and its derivatives. The *sph. colli profundus* forms a continuous transverse muscle layer (fig. 7c). In front of the ear the preauricular muscles have remained in broad primitive connection with their matrix, the *pars pre-auricularis sph. colli profundi*. The musculature of the face proper is yet little differentiated. The musculature of the snout, derivatives of the *pars oris sph. colli profundi* (fig. 7d & e), on the other hand, is differentiated and specialized. Note the muscle portions which are attached to the follicles of the supraciliary and cheek vibrissae (figs. 7a & c), to the mystacial vibrissae and to the vibrissae of the chin (figs. 7a, c & d). In contrast to the monotremes, the marsupials like the placentals possess a large spoon-shaped outer ear, with a well differentiated muscle apparatus composed of derivatives of both the post- and pre-auricular muscle groups (figs. 7a, b, c). A little shield (*scutulum*) of dense connective tissue has formed within the pre-auricular musculature, which allows these muscles to glide over the subjacent deep temporal fascia (figs. 7b & c). The scutulum of the opossum is, however, not as definite a structure as the similarly placed cartilaginous scutulum of representatives of certain orders of the placentals, such as the bats, lagomorph rodents (Leporidae and Ochotonidae), ungulates and carnivores (compare cat, fig. 11b; see further Huber, 1924/25, p. 370).

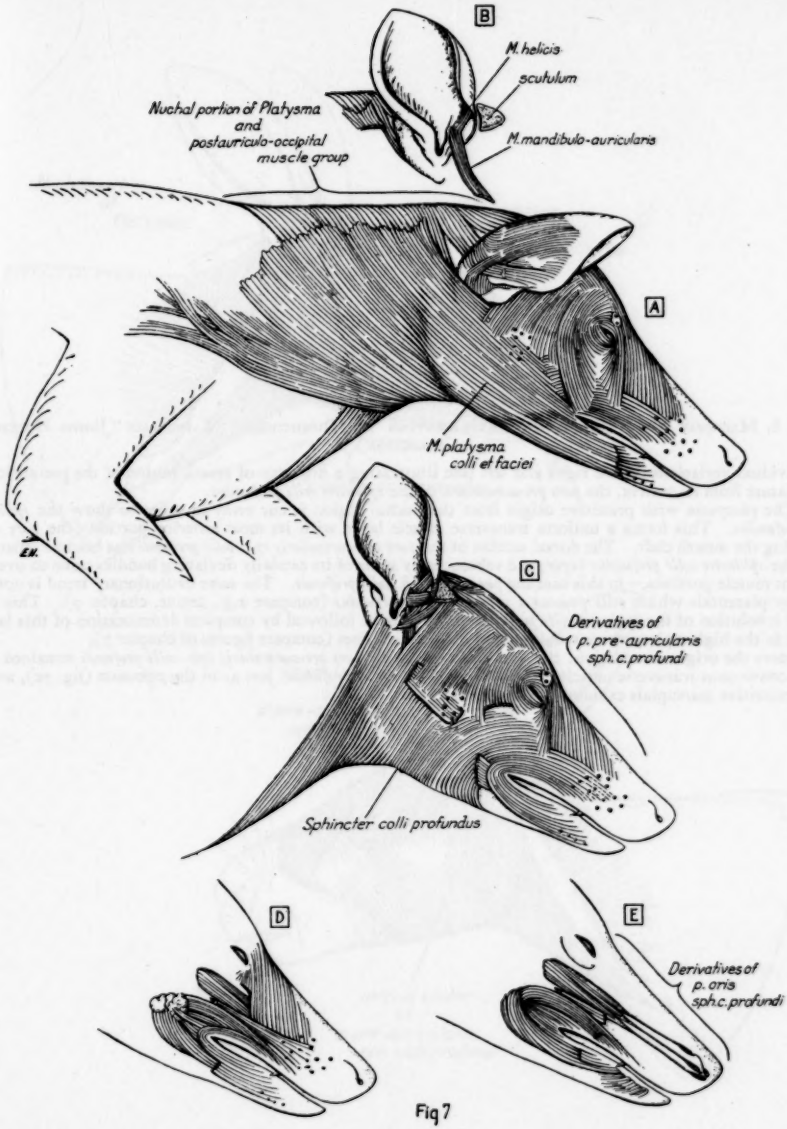

B
M. helicis
scutulum
Nuchal portion of Platysma and postauriculo-occipital muscle group
M. mandibulo-auricularis
A
M. platysma colli et faciei
C
Derivatives of p. pre-auricularis sph. c. profundi
Sphincter colli profundus
D
E
Derivatives of p. oris sph. c. profundi

Fig 7

FIG. 8. MACROPUS RUFUS (KANGAROO) REPRESENTING THE DIPROTODONT MARSUPIALS (JOHNS HOPKINS COLLECTION)

Individual variations on the right and left side illustrating a first step of emancipation of the pre-auricular musculature from its matrix, the *pars pre-auricularis* of the *sphincter colli profundus*.

a. The platysma with primitive origin from the nuchal region is cut away in order to show the *sphincter colli profundus*. This forms a uniform transverse muscle layer with its most anterior portion (the *pars oris*) encircling the mouth cleft. The dorsal section of the *pars pre-auricularis sph. colli profundi* has become separated from the *sphincter colli profundus* layer; and subsequently some of its caudally deviating bundles came to overlap adjacent muscle portions,—in this case the *pars auris sph. colli profundi*. The same evolutionary trend is noticed in many placentals which still possess a *sphincter colli profundus* (compare e.g., lemur, chapter 7). This first step of involution of the *sphincter colli profundus* layer may be followed by complete deterioration of this layer, as seen in the higher platyrrhine monkeys and in all catarrhines (compare figures of chapter 7).

b shows the original condition: the dorsal section of the *pars pre-auricularis sph. colli profundi* remained part of the continuous transverse muscle layer of the *sphincter colli profundus* just as in the opossum (fig. 7c), and in other primitive marsupials examined by the author.

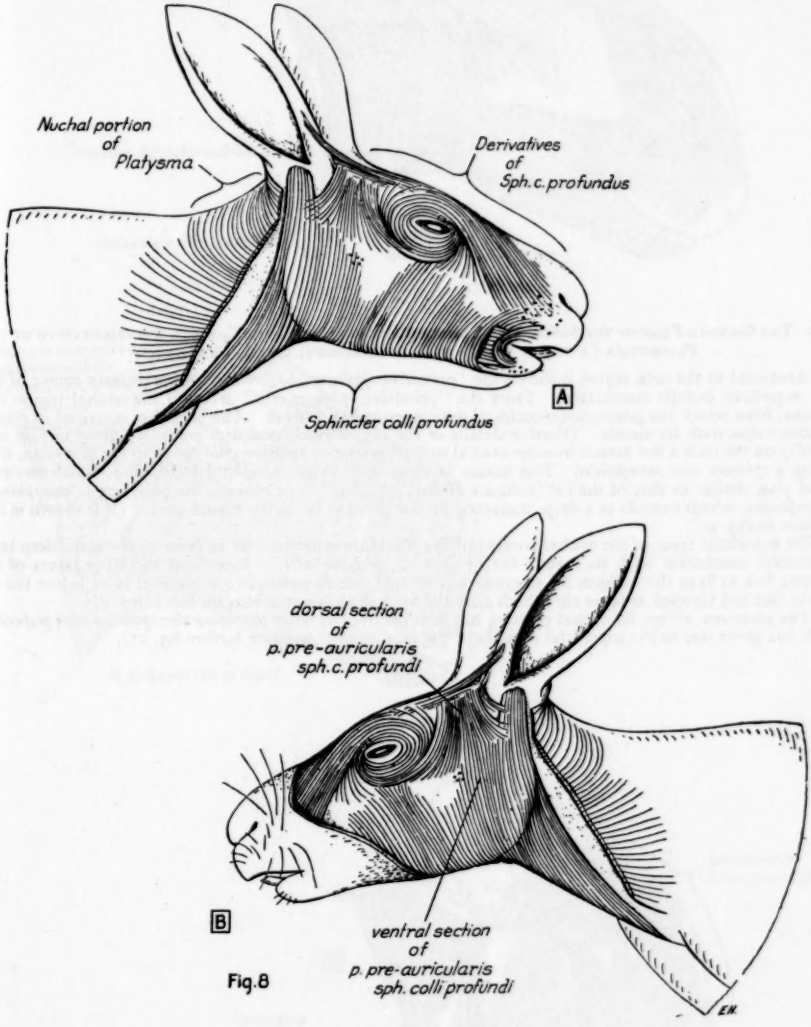

Nuchal portion
of
Platysma
Derivatives
of
Sph. c. profundus
A
Sphincter colli profundus
dorsal section
of
p. pre-auricularis
sph. c. profundi
B
ventral section
of
p. pre-auricularis
sph. colli profundi
E.H.

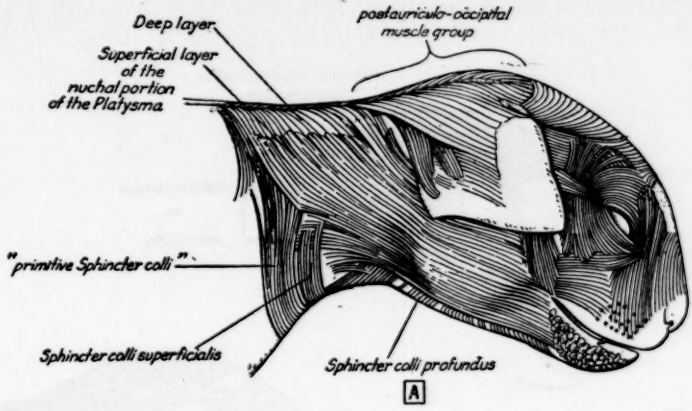
Fig. 8

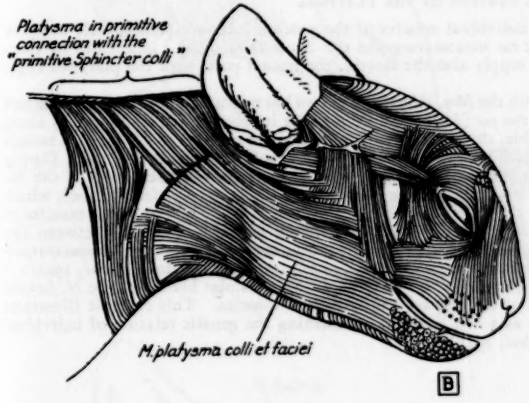
FIG. 9. THE GROUND PLAN OF THE SUPERFICIAL FACIALIS MUSCULATURE IN THE CAT AS A REPRESENTATIVE OF THE PLACENTALS (A AND B FROM THE SAME SPECIMEN; C FROM ANOTHER)

a. Restricted to the neck region is shown the "primitive *sphincter colli*," which is the primary source of the entire superficial facialis musculature. From the "primitive *sphincter colli*" arises in the nuchal region the platysma, from which the postauriculo-occipital muscle group has evolved. The latter has remained in primitive connection with its matrix. (Further details of the post-auriculo-occipital group are given in Fig. 10.) Ventrally on the neck a few muscle bundles cranial to the "primitive *sphincter colli*" overlap the platysma, thus forming a *sphincter colli superficialis*. This muscle layer is much better developed in the dog, which shows a ground plan similar to that of the cat (compare Huber, 1922/23). Just beneath the platysma is the *sphincter colli profundus*, which extends as a deep, transverse muscle layer as far as the mouth cleft. (It is shown in full extension in Fig. 9c.)

b. The superficial layer of the nuchal portion of the platysma is here cut off in order to show the deep layer in primitive connection with its matrix the "primitive *sphincter colli*." Superficial and deep layers of the platysma fuse to form the uniform *M. platysma colli et faciei*, which passes as a horizontal layer below the ear into the face and forward as far as the mouth cleft and for a short distance into the lower lip.

c. The platysma, except its nuchal portion, has been removed in order to expose the *sphincter colli profundus*, which has given rise to the superficial muscles of the face proper (compare further fig. 11).


Deep layer
Superficial layer of the nuchal portion of the Platysma
postauriculo-occipital muscle group
"primitive Sphincter colli"
Sphincter colli superficialis
Sphincter colli profundus
A


Platysma in primitive connection with the "primitive Sphincter colli"
M. platysma colli et faciei
B

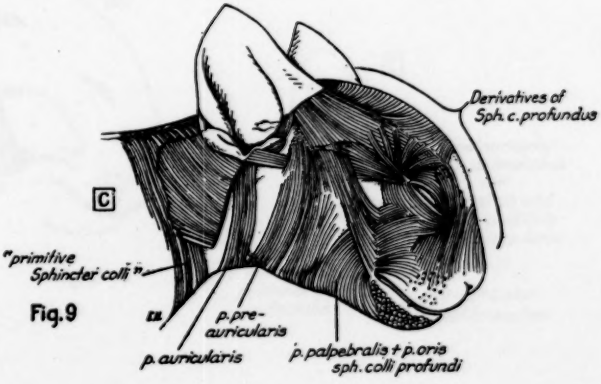

Derivatives of Sph. c. profundus
C
"primitive Sphincter colli"
p. pre-auricularis
p. auricularis
p. palpebralis + p. oris sph. colli profundi

Fig. 9

FIG. 10. CAT (CONTINUED), SHOWING THE DERIVATION OF THE POST-AURICULO-OCCIPITAL MUSCLE GROUP FROM THE NUCHAL PORTION OF THE PLATYSMA

According to this evolution we find the individual muscles of the post-auriculo-occipital muscle complex (including part of the extrinsic and intrinsic ear musculature and the *M. occipitalis* (a)) innervated by post-auricular branches of the *N. facialis*, which supply also the matrix, the nuchal portion of the platysma (figs. 10b and c).

d & e. A muscle portion in continuation with the *Mm. obliqui et transversi* has migrated from the convex surface of the ear cartilage to the anterior border of the ear (*M. helicis*) from where it proceeded in its migration along the cartilaginous ear tube as far as the mandible, thus invading the pre-auricular territory. This second muscle section forms the *M. mandibulo-auricularis*, which has become firmly attached to the mandible (fig. 10d). During the migration this muscle-tract carried its nerve supply with it. Hence the peculiar innervation of the *M. helicis* and *M. mandibulo-auricularis* through a branch of the *rami auriculares posteriores n. facialis* (fig. 10e), which passes from behind in a wide detour around the concha of the ear until it reaches these two small muscles to which it supplies terminal twigs. While in the cat primitive persisting muscle connections between the *M. mandibulo-auricularis* and the *M. helicis* (fig. 10d), and between the latter muscle and the *Mm. obliqui et transversi* on the convex surface of the ear cartilage still indicate the trail of migration, in the dog (Huber, 1922/23) these last muscle connections are lost, and the innervation through a post-auricular branch of the *N. facialis* remains the sole, though a clear, indication of the genetic origin of these muscles. This example illustrates beautifully that the nerve supply may serve as a safe guide in establishing the genetic relation of individual muscles within muscle groups (compare Huber, 1925).

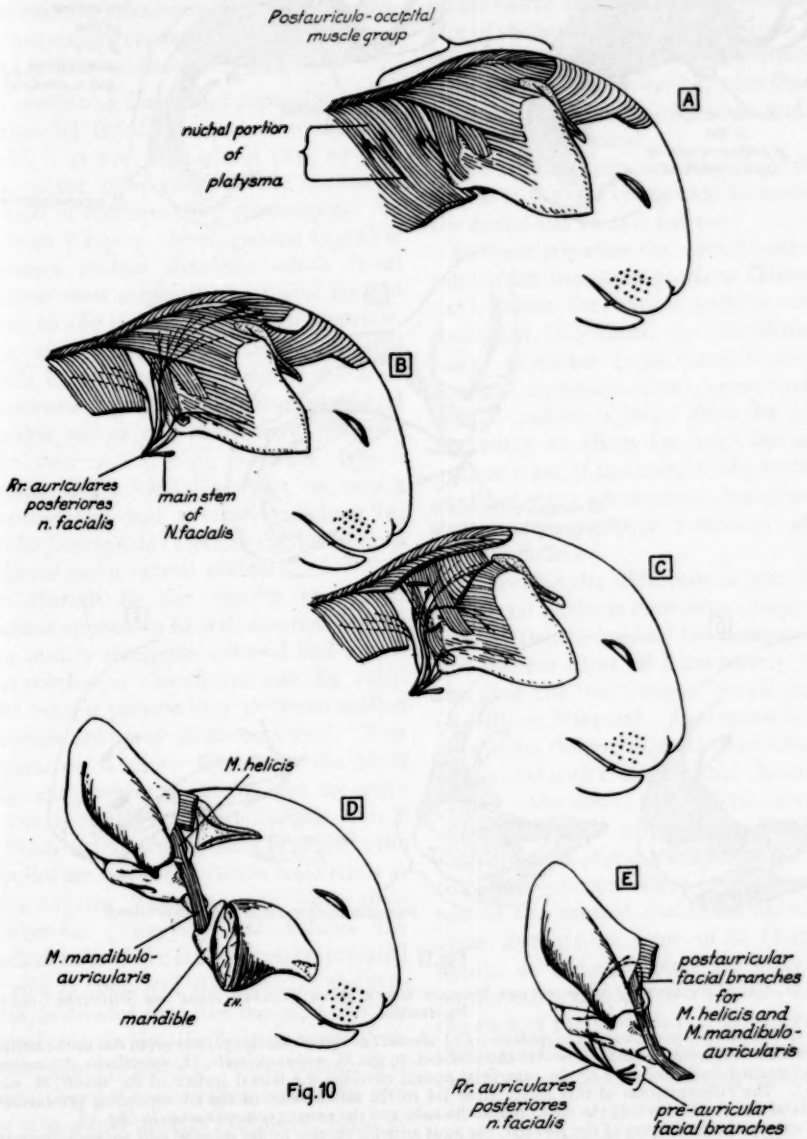

Postauriculo-occipital muscle group
nuchal portion of platysma
A
B
Rr. auriculares posteriores n. facialis
main stem of N.facialis
C
M. helicis
D
M. mandibulo-auricularis
mandible
E
postauricular facial branches for M. helicis and M. mandibulo-auricularis
Rr. auriculares posteriores n. facialis
pre-auricular facial branches

Fig. 10

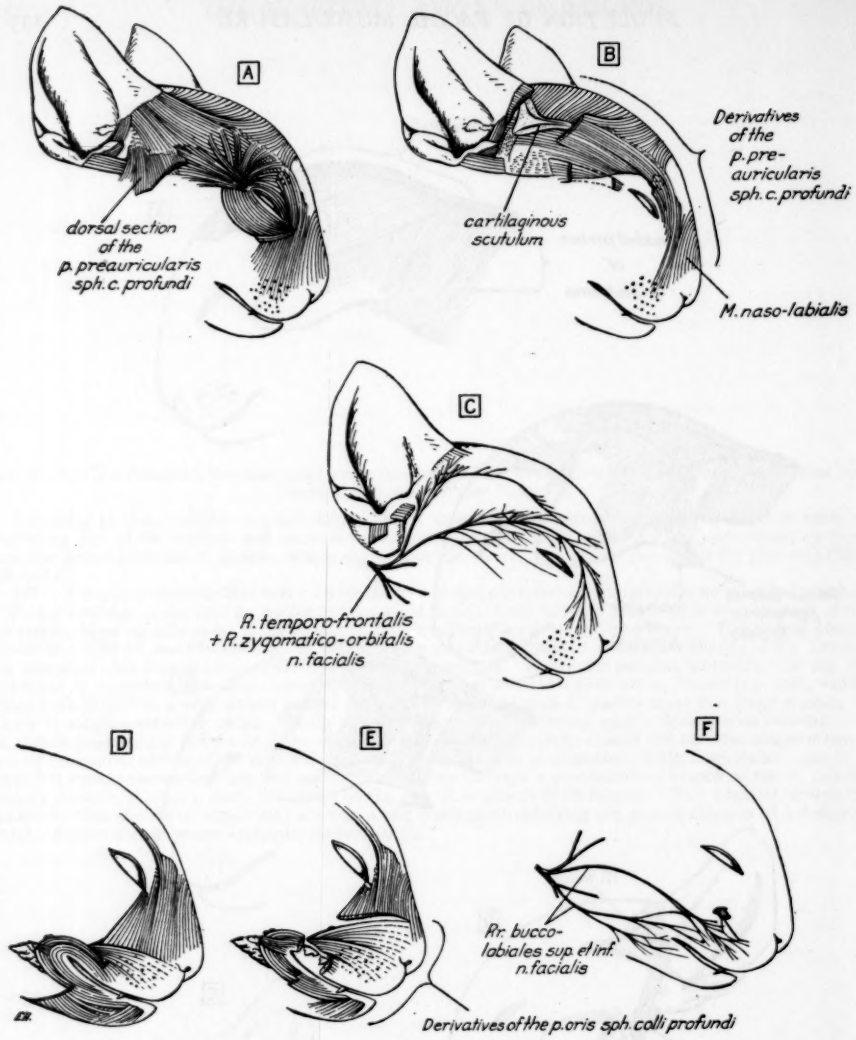


Fig. 11

FIG. 11. CAT (CONTINUED), SHOWING THE MUSCLES WHICH HAVE EVOLVED FROM THE SPHINCTER COLLI PROFUNDUS

a & *b*. The *pars pre-auricularis* of the *sphincter colli profundus* (compare also fig. 9c) has given rise to the muscle-complex located in front of the ear and over the forehead, to the *M. orbicularis oculi*, *M. superciliaris*, *M. auriculo-labialis* (omitted in figure), and to the superficial muscle covering the lateral surface of the snout (*M. naso-labialis*). The differentiation of this musculature led to the ramification of the corresponding pre-auricular branches of the *N. facialis*, i.e., the *ramus temporo-frontalis* and the *ramus zygomatico-orbitalis* (fig. c).

d & *e* show the derivatives of the *pars oris*, the most anterior portion of the *sphincter colli profundus* (compare fig. 9c). These muscles (*M. orbicularis oris*, *M. buccinator*, *M. maxillo-naso-labialis* and *M. mentalis*) are innervated by the *rami bucco-labiales superior et inferior* of the *N. facialis* (fig. f). It should be mentioned that in fig. 11d the *M. naso-labialis*, which does not belong to this group (compare figs. 11a–c), is left in place simply to show the topographic relationship to the two portions of the *M. maxillo-naso-labialis*, which are separated by the *M. naso-labialis*. The innervation given in figs. 10b, c and e; 11c and f, is based on morphological investigation (Huber, 1918, 22/23) verified by experiments (Huber, 1924; Huber and Hughson, '25).

II. CORRELATION OF THE DEVELOPMENT OF THE MOTOR NUCLEUS OF THE N. FACIALIS WITH THE EXPANSION AND DIFFERENTIATION OF THE SUPERFICIAL FACIALIS MUSCULATURE IN MAMMALS

Considering the unique expansion of the superficial facialis musculature in mammals, it is not astonishing that we find the motor component of the *nucleus n. facialis* of corresponding dimensions.

From Kappers' investigations (1910) it becomes evident that the whole facial nucleus must originally have been located close to the floor of the fourth ventricle, near the primitive taste centre. It still holds this position in some of the *lower Vertebrates* (fig. 12a). In others the facial nucleus shows the tendency to split up into two nuclei, e.g., in fishes, into a frontal and a caudal nucleus, or into a fronto-dorsal and a ventral nucleus; or, in the Sauropsida (reptiles and birds) into a dorsal and a ventral nucleus.

Although in the reptiles the facial nucleus appears to be still continuous, one can readily recognize a dorsal and a ventral portion, of about equal size (fig. 12b). The ventral portion may be found shifted ventralward away from the dorsal. This separation is more distinct in the birds (fig. 12c), where the two nuclei are quite a distance apart (compare Kappers, 1910).

From such an arrangement as found in the reptiles we can easily derive conditions as seen in the *Monotremes*. In both *Ornithorhynchus* (*Platypus*) and *Echidna* the nuclear mass of the facial, greatly increased in size as compared with that of the reptiles, is divided into two nuclei, a distinct dorsal and an equally distinct ventral nucleus (figs. 13a and b). Their expansion is frontalward into the reflex area of the motor trigeminal nucleus (Kappers, 1920, p. 533). While the dorsal nucleus remained in its primitive dorsal position, the ventral nucleus has shifted further ventralwards than in the reptiles. However, it still holds a position midway between the floor of the fourth ventricle and the ventral surface of the brain stem (Kappers, 1910, p. 81 for *Echidna*), or (according to Koelliker, 1901, fig. 17 for *Echidna;* fig. 5 for *Ornithorhynchus*; Hines, 1929, figs. 16 and 17) slightly more ventral.

The two monotremes show some difference as to the relative size and formation of the dorsal and ventral nucleus.

In *Ornithorhynchus* the dorsal nucleus is subdivided into two portions (Hines, p. 221), while the ventral nucleus remains undivided (Koelliker, p. 36; Hines, p. 222). Koelliker (1901) and Hines (by personal communication) agree that the ventral nucleus is larger than the dorsal. According to Hines (p. 222) the dorsal nuclear mass, if projected to the surface of the floor of the 4th ventricle, has about the same antero-posterior extension as the ventral nucleus.

In *Echidna* the difference in size of the two facial nuclei is even more conspicuous than in *Ornithorhynchus*, the compact ventral nucleus being of considerably larger size than the less compact dorsal nucleus (Koelliker, Kappers). In contrast to *Ornithorhynchus* the ventral nucleus of *Echidna* is subdivided into three portions (Koelliker, p. 97). Moreover, the sagittal extension of this nucleus is peculiar (Koelliker, Kappers) in that it extends as a continuous column of large motor cells from far behind the root of the facial nerve to a great distance in front of it (Kappers, 1910). In the marsupials and placentals, on the other hand, it lies entirely behind the root of the *N. facialis*. However, the characteristic position of this nucleus in *Echidna* is not due to a shifting in a frontal direction but is merely the result of its frontal enlargement (Kappers, 1910, p. 84 footnote). The enormous size of the nuclear mass of the facial, especially in

Echidna (compare Kappers, 1920, p. 532) coincides with the development of the superficial facialis musculature in these animals (Ruge, Schulmann, Boas and Paulli, Huber). Considering the small size of the monotremes the heavy and coarse muscle bundles of their facial muscle group form a very large bulk (figs. 5, 13c and d). These muscles not only supply the area of the head but cover in heavy sheets the neck and expand caudalward into the domain of the *panniculus carnosus*. In both *Ornithorhynchus* and *Echidna* the superficial facialis musculature has gained an extensive connection with the fore limb. These latter muscle portions evidently have great functional importance. The extension and bulk of the superficial facialis musculature of *Echidna* greatly exceeds that of *Ornithorhynchus*. This is the explanation for the relatively smaller size of the facial nuclei and *N. facialis* in *Ornithorhynchus*.

While the large ventral facial nucleus of the monotremes presumably represents the motor component, there is good reason to believe that the dorsal nucleus is also motor, at least in part. In *Ornithorhynchus*, as Hines emphasizes, the cells of the dorsal nucleus appear too large and too numerous for visceral effector cells (Hines, 1929, p. 222). Moreover, the comparatively large size of the dorsal nucleus in *Ornithorhynchus* makes it very likely that many of its cells together with the cells of the ventral facial nucleus are destined for the superficial facialis musculature. However, we have no definite knowledge in regard to the functional rôle of these two nuclei (Kappers, 1920, p. 534, concerning *Echidna;* Hines, 1929, p. 222, concerning *Ornithorhynchus*). Up to this time no experimental approach towards the solution of this problem has been made.

In the *Marsupials* and *Placentals* only a very small part of the facial nucleus, mainly of visceral nature, retains the dorsal position, while the unquestioned motor part, enormously increased in size, has shifted ventralward (fig. 14a) probably through neurobiotactic influences, nearer to the reflex tracts which bring in impulses from the mouth, nose, eyes and ears and also closer to the decussation of the facial pyramidal tracts, which transmit cortical impulses to the facial nucleus (Kappers, 1908, '10, '20/21, '27). In contrast to the monotremes this motor facial nucleus has attained a definite ventral position, lying almost directly on the base of the brain stem (Kappers, 1910, p. 84).

The phylogenetic rearrangement (ventral shifting) of the motor part of the facial nucleus in marsupials and placentals is reflected in the embryological development, whereby this nucleus shifts from a more dorsal position into its definite ventral position. During the displacement of the nucleus, the *radix n. facialis* at its emergence from the medulla oblongata evidently remains fixed, and this phenomenon leads to the peculiar formation of the facial loop, usually around the nucleus of the abducens nerve (fig. 14a).

The nuclear origin of the motor elements of the facial nerve has for a long time been subject to controversy. In order to explain the well-known fact that in cases of facial palsy of central origin in man, the mimetic muscle group supplied by the temporofrontal and zygomatico-orbital facial branches remains unaffected, several authors have assumed a dual nuclear origin of the facial nerve. Thus it was the belief of Mendel (1887) that additional fibres to the facial arise in the nucleus of the oculomotor nerve, while Duval, Testut and others thought that the facial, as it looped over the abducens nucleus, received a contingent of fibres from it for the upper facial branches. Pure histological, as well as experimental—and clinical—his-

tological studies by a series of investigators, however, have brought conclusive evidence against a dual origin of the facial nerve. They proved that the motor part of the *nucleus facialis* is the sole source of fibres for the entire motor facial nerve.

As a result of the differentiation of the superficial facialis musculature and the subsequent ramification of the involved facial branches, we find subdivisions in the motor facial nucleus (fig. 14b).

A series of studies by Van Gehuchten ('93, '98), Cajal ('95), Marinesco ('98, '99), Bruce and Pirie ('08), Yagita ('10), Papez ('27), and others has been undertaken to investigate the topography of these subdivisions and to correlate them with the differentiations in the peripheral facialis field. In their conclusions concerning the nature of the subdivisions the various authors do not agree. The question is whether the subdivisions of the nucleus correspond to a phylogenetic or to a functional grouping of the superficial facialis musculature with the corresponding peripheral facial branches involved, or whether additional factors influencing the development of the central nervous system may here play a rôle. According to the most recent publications of Papez (1927) the plan of subdivision of the facial nucleus seems to follow the phylogenetic differentiation of the superficial facialis musculature and the consequent branching of the facial nerve (fig. 14c) such as has been brought out through morphological investigations of the author (Huber, 1922/23; Huber and Hughson, 1926). Additional investigations on the facial nucleus of the cat undertaken by DeGaris have not come to a definite conclusion (DeGaris, *Anat. Rec.*, 1929, abstract).

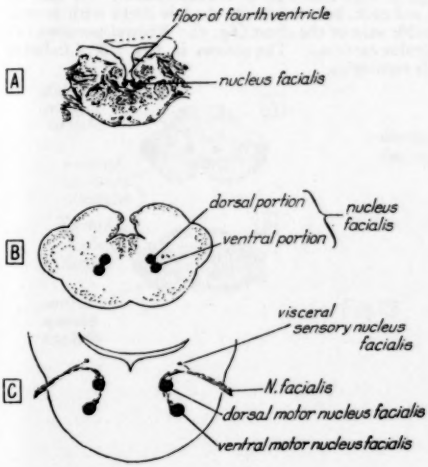


Fig. 12

FIG. 12. CROSS SECTIONS THROUGH THE MEDULLA OBLONGATA AT THE LEVEL OF THE NUCLEUS FACIALIS

a. *Gadus* (cod) as a representative of the bony fishes (after Kappers, 1910). The *nucleus facialis* is seen in a primitive dorsal position close to the floor of the 4th ventricle. Only part of this nucleus is motor, destined to supply the facialis musculature, which is not extensive in the fish (compare fig. 1).

b. The facial nucleus in reptiles (modified after Kappers). The *nucleus facialis* has increased in size in correlation with the expansion of the superficial facialis musculature (compare fig. 3), and is subdivided into a dorsal and a ventral portion.

c. The facial nucleus in birds (combined from Kappers, 1910, and J. Sanders, 1929). The dorsal and the ventral portion of the nucleus facialis are more clearly separated, thus forming two distinct nuclei.

FIG. 13. THE NUCLEAR MASS OF THE N. FACIALIS IN THE MONOTREMES, ORNITHORHYNCHUS (A) AND ECHIDNA (B), WITH ADDITIONAL FIGURES C AND D ON THE FACIAL MUSCULATURE OF ECHIDNA, TO ILLUSTRATE THE CORRELATION BETWEEN THE SIZE OF THE NUCLEUS FACIALIS AND THE BULK OF THE FACIALIS MUSCULATURE

a. The facial nuclei of *Ornithorhynchus* (after Hines, 1929).
b. The facial nuclei of Echidna (after Kölliker, 1901).
There are two distinct facial nuclei, the ventral having shifted further ventralwards than in the reptilian plan. In *Ornithorhynchus* the dorsal nucleus is subdivided into two portions, while the ventral nucleus remains undivided. In *Echidna* it is the dorsal nucleus which remains undivided, while the ventral nucleus shows three subdivisions. In both monotremes the ventral nucleus is found larger than the dorsal. This is more conspicuous in *Echidna*. A comparison with figure 12b shows the great increase of the nuclear mass in the monotremes,—an increase which coincides with the enormous expansion of the superficial facialis musculature in these animals (compare fig. 5 and 13c and d with fig. 3). The facial nuclei of *Echidna* (fig. *b*) exceed in size those of *Ornithorhynchus* (fig. *a*). This is in accord with the fact that in *Echidna*, the superficial facialis musculature, composed of heavy coarse muscle bundles, is more extensive and larger in bulk than that of *Ornithorhynchus*. As seen in figures 13c and d it is not confined to the region of the head and neck, but inserts into the fore limbs with several powerful portions which cover, in their origin, a considerable area of the chest (fig. *c*). Ventral portions (*d*) likewise extend caudalward into the domain of the panniculus carnosus. The arrows in figs. *c* & *d* indicate the border line between the two genetically distinct muscle territories.

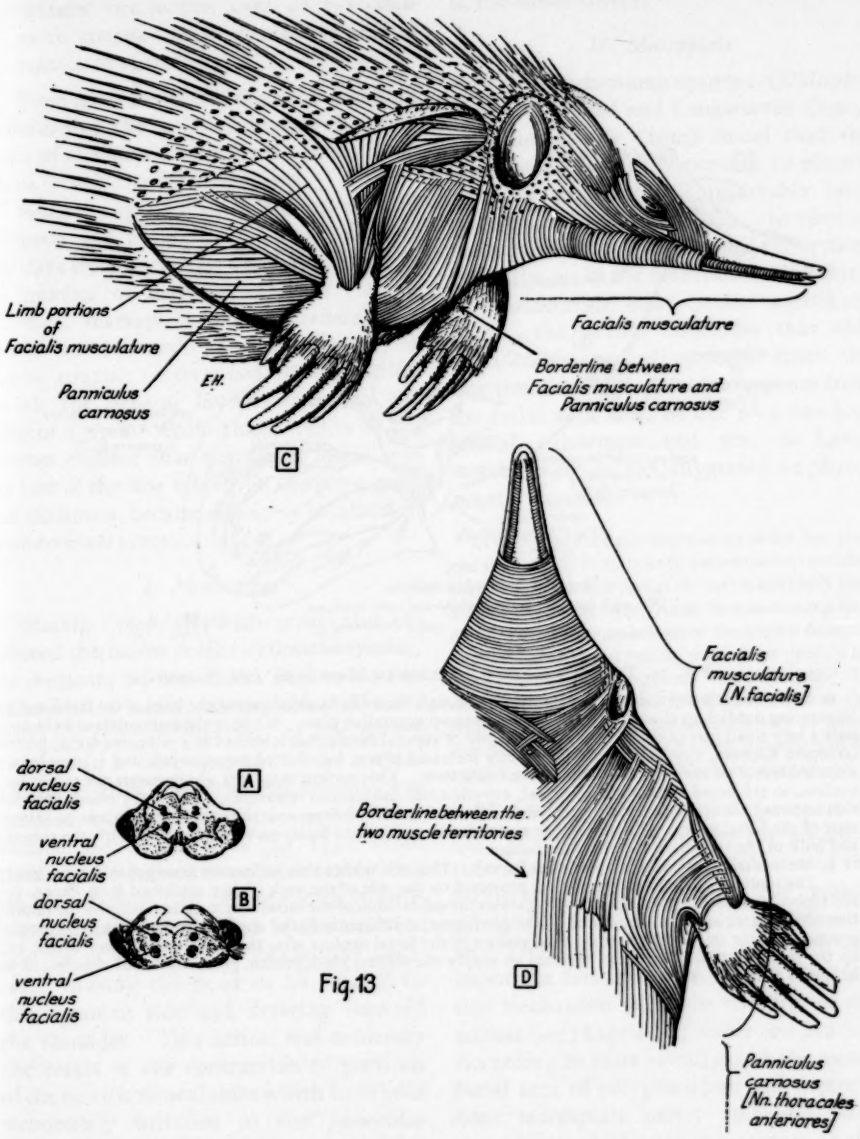

Limb portions of Facialis musculature
Panniculus carnosus
E.H.
Facialis musculature
Borderline between Facialis musculature and Panniculus carnosus
C
dorsal nucleus facialis
ventral nucleus facialis
A
dorsal nucleus facialis
ventral nucleus facialis
B
Facialis musculature [N. facialis]
Borderline between the two muscle territories
D
Panniculus carnosus [Nn. thoracales anteriores]

Fig. 13

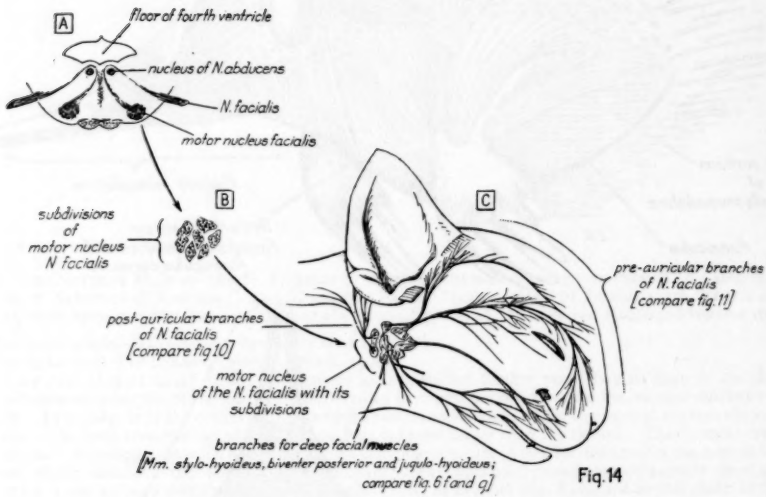

A
floor of fourth ventricle
nucleus of N. abducens
N. facialis
motor nucleus facialis
B
subdivisions of motor nucleus N facialis
C
pre-auricular branches of N. facialis [compare fig. 11]
post-auricular branches of N facialis [compare fig 10]
motor nucleus of the N. facialis with its subdivisions
branches for deep facial muscles [Mm. stylo-hyoideus, biventer posterior and jugulo-hyoideus; compare fig. 6 f and g]
Fig. 14

FIG. 14. THE MOTOR FACIAL NUCLEUS IN MARSUPIALS AND PLACENTALS

a. Schematic representation of a cross section through the medulla oblongata at the level of the facial nucleus, illustrating conditions characteristic of the marsupio-placentalian plan. While in the marsupials and placentals only a very small part of the facial nucleus, mainly of visceral nature, has remained in a primitive dorsal position (compare Kappers, 1910), the rest, enormously increased in size, has shifted ventralwards and is now situated almost directly on the ventral surface of the brain stem. This nuclear mass (see *a*) represents the motor facial nucleus, as evidenced through histological, experimental and clinical researches. The fibers which arise from this nucleus pass upwards, loop around the nucleus of the *N. abducens* and then turn lateralwards to form the root of the facial nerve. The size of the motor facial nucleus and facial nerve corresponds with the extension and bulk of the superficial facialis musculature.

b. Motor facial nucleus of the cat (after Papez). The cells within this nucleus are arranged in definite groups.

c. The motor facial nucleus in the cat projected on the side of the neck (figure combined from Papez, 1927, and Huber). According to Papez' investigations the subdivision of the facial motor nucleus follows the ramification of the facial nerve as determined by the phylogenetic differentiation of the facialis musculature. From the groups of motor cells of the various subdivisions of the facial nucleus arise the motor nerve fibers which build up the peripheral facial branches destined to supply the various phylogenetic groups of facial muscles, as seen in figures 6, 10 and 11.

III. LOCALIZATION OF THE FACIALIS FIELD WITHIN THE MOTOR AREA OF THE CEREBRAL CORTEX IN MONOTREMES, MARSUPIALS AND PLACENTALS

Even more important than the questions concerning the facial nucleus, is the problem of the motor localization of the facial area within the cerebral cortex.

Since the epoch making pioneer work of Fritsch and Hitzig (1870) a vast number of data from studies on the motor cortex in a number of mammalian types (monotremes, marsupials and placentals) has been accumulated. The facial area has been roughly determined in connection with the general investigations on the motor cortex. From these studies it becomes evident that the motor facial area is one of the first which, in the phylogeny of mammals, became definitely localized in the cerebral cortex.

I. Monotremes

Martin (1898/99) with great care explored the motor cortex in *Ornithorhynchus*. Movements of the facial field were obtained most easily. Stimulation of most parts of the anterior half of the cortex resulted in a "screwing-up" of the contralateral eyelids, but this movement was aroused with the weakest current at a smaller area further back (fig. 15). From the large ill-defined responsive motor area on the anterior half of the cortex Martin also obtained contraction of the anterior portion of the opposite "*panniculus carnosus*," causing the head to be rotated to the opposite side and drawing forward the shoulder. This action was evidently the result of the contraction of portions of the facialis musculature which have been erroneously included in the *panniculus carnosus* (compare Huber, 1924, p. 178 ff.).

Martin made the observation that in *Ornithorhynchus* facial and fore limb areas partly coincide, and that the hind limbs and tail apparently have no representation in the motor cortex.

II. Marsupials

In the pouch-young opossum (*Didelphys virginiana*) Weed and Langworthy (1925) and Langworthy (1927) found that the facial area becomes responsive to electrical stimulation at a considerably later stage than the fore limb area. In view of the precedence in structural development and early use of the fore limbs, and taking in consideration some further significant points, the author concludes that this considerably earlier response from the fore limb in contrast to the response from the facial area must be due to a developmental adjustment and not, as Langworthy (1927, p. 170) suggested, to phylogenetic sequence.

In regard to the early functioning of the fore limb one should refer to Hartmann's observation that after the ten day gestation period the very immaturely born young, measuring only 11 mm. in crown-rump line, crawl without any assistance of the mother from the vaginal orifice to the pouch, where they quickly become attached to the nipples. In crawling they use the fairly well-developed fore limbs, while at this stage the hind limbs are represented merely by extensive buds. Kangaroo young reach the pouch of the mother in the same manner (C. Hartmann, 1920).

Within the facial area of the opossum (fig. 16) movements of the ear musculature, of the *M. orbicularis oculi* and of the vibrissae can be elicited. The muscle group which moves the facial vibrissae is well represented in accordance with the important functional rôle which this tactile mechanism plays in the life of the animal (see chapter VI, Huber and Smith). According to most investigators the motor facial area of polyprotodont and diprotodont marsupials partly coincides with areas from which also movements of the fore limbs are obtained. The latter appear still to have partial representation in the corpus striatum (Rogers, 1924).

As to the cortical representation of the hind limbs, the various investigators do not agree in their findings. Several authors, Herrick and Tight (1890), Ziehen (1897), Flashman (1907) and C. and O. Vogt (1906/07) reported hind limb movements, which were, however, obtained with difficulty and only through application of stronger current. Such movements when obtained were more diffuse compared with the fore limb movements. Cunningham (1897/98) and several more recent investigators (Rogers, 1923, '24; Gray and Turner, '24; Weed and Langworthy, '25; Langworthy, '27), on the other hand, were unable to obtain in the opossum movements of the hind limbs, trunk or tail, despite careful exploration of the whole cerebral cortex. Future investigations will have to give proof whether there possibly occur progressive individual variations, in which part of the motor center for the hind limbs has shifted into the cortex. This seems a possible explanation for the positive results of the first group of investigators.

III. Placentals

There are a series of orders and suborders of the placentals which have never been subjected to experimentation, while of the others only one or a few representatives have been studied.

1. Insectivores. Of this order, only the hedgehog (*Erinaceus europaeus*) has been investigated. The results obtained by the various investigators differ widely. They are in part uncertain, and incomplete. For example, Mann (1896) failed to obtain response from any part of the facialis musculature, while Ziehen (1897) and C. and O. Vogt (1906/07) observed no movements of the *M. orbicularis oculi* nor of the ear musculature. Evidently those facial muscles which during the life of the insectivores, play the greatest rôle (i.e. the muscles of the snout) are the best represented (Ziehen; Probst, 1901; C. and O. Vogt), while the other muscles of the facialis group do not readily respond (see Ziehen, '99, p. 169, in contrast to '97). The snout musculature appears to be bilaterally represented (C. and O. Vogt).

Besides the facial area, areas for the fore and also for the hind limbs have been located. The movements hereby elicited were isolated, uncorrelated movements of certain muscle groups only, and not easily obtained.

2. Bats. C. and O. Vogt (1906/07) found in the fruit bat (*Pteropus*) the "head segment" with the facial area far more extensive and more responsive than the leg areas. Various subdivisions of the facial area were mapped out, which responded with three different kinds of "rhythmic movements" of the muscles of the snout, *M. orbicularis oculi* and ear musculature.

3. "Rodents," (including the rodents in the strict sense, and the lagomorph or duplicident rodents). The investigations on the motor cortex of mouse, rat, rabbit, guinea-pig and some further rodents by various authors (Ferrier, 1873, '74, '80/86; Fürstner, '76; v. Bechterew, 1886/87, '87, '11; Exner and Paneth, '87; Herrick and Tight, '90; Mann, '96; Mills, '96; Ziehen, '97; Simpson, 1914, '15; Lashley, '21; W. K. Smith, unpublished) show that the motor cortex of the rodents is ill-defined and variable. It is still on a very primitive evolutional level (compare Herrick, 1926, p. 165). The data so far obtained, however, are very incomplete, in part contradictory and as yet little correlated.

Interesting are the results of stimulation experiments on new-born and very young rabbits in comparison with new-born and near-term fetuses of guinea-pigs. In the rabbit Tarchanoff (1878) did not obtain

any movements until the animals were about eleven days old. Then it was possible to elicit fore limb and masticatory movements. Only considerably later were movements of the hind limbs obtained. According to Tarchanoff (p. 860/861) the area for masticatory movements, in which also the orbicularis oris-buccinator group of the facialis musculature is involved, is in the young rabbit more responsive than the fore limb area, whereas the hind limb area did not give regular response. While Tarchanoff and several subsequent authors claim in the rabbit a responsive hind limb area, besides the areas for the fore limb, facial and masticatory musculature, Mills ('96), after examination of a large series of different breeds of young and adult rabbits, emphatically denies the existence of a responsive hind limb area in this animal. Mills found the rabbit in striking contrast with the guinea-pig, rat and mouse. In these latter rodents he could confirm the general motor localization such as previously found by Ferrier, who located a hind limb area in addition to the other areas (compare Mills, p. 28). Most significant is the fact that in the rabbit (compare v. Lenhossék, 1889; Simpson, '14, '15) as in a series of further rodents (compare v. Lenhossék, '89; Goldstein, 1903/04; Wallenberg, '03/04; van der Vloet, '06; King, '10; Simpson, '12/13, '14, '15; Ranson, '13, '14; Linowiecki, '14; Reveley, '15) the cortico-spinal tract could be traced, though greatly reduced at least as far as the lumbar part of the spinal cord. In some cases this tract extended even to the sacral sections of the cord. Thus there evidently exists in these "rodents," including the rabbit, a definite anatomical basis for positive cortical motor response of the hind limbs.

Motor response is obtained in the guinea-pig much earlier than in the rabbit, occurring at birth or within a few hours after birth (Tarchanoff, 1878; Langlois, '89; Mills, '96), or even shortly before birth (Tarchanoff). In new-born guinea-pigs Tarchanoff and Langlois obtained movements of mastication, fore limb movements, and (with stronger current: Langlois) also movements of the hind limbs. By far the easiest to obtain were the masticatory movements (Tarchanoff, Langlois, Mills), in which, presumably besides the masticatory musculature, the orbicularis oris-buccinator group of the facialis musculature are involved just as in the rabbit.

The great difference in first appearance of motor responses in the guinea-pig compared with the rabbit, rat and mouse is undoubtedly correlated with the difference in the state of general development in which these rodents are born. While rabbits, rats, and mice are born in a very immature and helpless state, the guinea-pigs come into the world in a relatively mature condition with a well developed coat of fur and with open eyes, able to run around. Von Lenhossék (1889) also emphasizes the fact that in the new-born guinea-pig the tracts of the spinal cord, including the pyramidal system, are further advanced in development and larger in size than in the new-born rabbit or mouse.

It is noteworthy that in both rabbit and guinea-pig the masticatory movements prevail over the movements of the fore limbs. This is in striking contrast to results obtained in the opossum (referred to above), cat and dog (see later). It is very likely that in the various mammalian types developmental adjustments of the various motor centers take place according to the differences in behavior during early postnatal life (compare also Mills' extensive studies on the psychic development of various types of placentals, 1894, '95, '96).

4. Ungulates. The motor cortex of the sheep and goat as representatives of this

order have been studied by Marcacci (1877), Ziehen ('99), Dexler and Margulies (1906), Simpson and King ('11), Bianchi ('20), Bagley ('22), and W. K. Smith (unpublished). The results obtained by the various investigators are in part contradictory and indefinite. A series of responsive areas which show considerable individual differences have been mapped out. Among these is a facial area, which gives response of the contralateral and in part bilateral facialis musculature. Besides the main facial area Bagley located an additional well defined area which readily responded with homolateral contractions of facial muscles of the mouth. In agreement with Marcacci and in contrast to Simpson and King, Bagley found the facial area more responsive than the other areas. According to most authors, response from the fore legs is more easily obtained than from the hind legs. Marcacci was unable to obtain movements from the latter.

5. Carnivores. Of special interest are the developmental studies on the motor cortex of cat and dog. Because of the divergence in reported results the findings on these two animals will now be given separately.

The cortex of *cats* at birth and for several days after did not respond to electrical stimulation according to Mills (1896), but in some cases the cortex was functionally active before the eyes opened, i.e., before the ninth day. The centers for the fore limbs were found responsive earlier than those for the hind limbs, and head movements could be obtained only at a later date than movements of the limbs.

Among the subsequent investigators Weed and Langworthy (1926), and Langworthy ('27) obtained fore limb movements in kittens at birth (fig. 17a), while, strangely enough, hind limb movements could not be obtained until the kittens were sixteen days old, and the "facial area" did not respond to electrical stimulation until twenty-one days of age. The animals were, as in Mills' experiments, stimulated under ether anesthesia, which the investigators considered essential in order to exclude the possibility of spontaneous movements being interpreted as due to the results of electrical excitation (Weed and Langworthy, p. 95).

Soltmann (1876), who deserves credit for having initiated these studies on the motor cortex of new-born and very young animals, came to the conclusion that the development of function of the motor cortex is determined by the time of opening of the eye slit.

In *dogs*, Soltmann found the motor cortex not responsive until the tenth day after birth, when the first fore limb movements were obtained. At the thirteenth day, movements of the hind limbs together with fore limb movements could be elicited. But it was not until the sixteenth day that movements from the facial area were obtained. Soltmann used in his experiments on puppies ether or chloroform as anesthetics or gave subcutaneous injections of morphia.

Later, Ferrier (1880/86) agreed that in puppies no limb movements are obtained until after the opening of the eyes, usually about the eighth day, stating that generally the cortical centers in the dog do not react till about the tenth day, and that the centers of the fore limbs become excitable before those of the hind limbs.

Mills ('96) also came to the conclusion (p. 9) that there is no proper functional cortical development in dogs before the eyes open, which seldom occurs before the tenth to the thirteenth day (p. 17). He confirmed Soltmann in that the movements of the head as a whole and of its various parts are developed later than those of the limbs. However, in disagreement with

Soltmann and Ferrier he found that in most, though not in all of his cases the hind leg was functionally active at a somewhat earlier date than the fore limb,—an observation which could not be confirmed by subsequent investigators. In the case of large dogs, as the St. Bernard, the cortical motor centers became functionally active at a later date than in small breeds, like the "terriers" or in mongrels, an important observation which seems in harmony with the more rapid physical and psychic development of the latter (p. 9, 10, 21). In agreement with Soltmann, Mills (p. 16) emphasizes that the localization at first is somewhat indefinite, but gradually, though rapidly, becomes better defined. He found the principal centers active within the first thirty days of life; most of them earlier (p. 10). Mills, like his forerunner, stimulated his puppies under anesthesia using ether.

Paneth (1885), however, using no anesthesia, obtained positive results in dogs within 24 to 48 hours after birth. These puppies responded to electrical stimuli prevailingly with fore limb movements, while hind limb movements were sparingly obtained.

Subsequent investigators, Michailow (1910) and v. Bechterew (1911), in dogs, likewise obtained positive results during the first few days of postnatal life. They were able at this time to locate electrically excitable areas for both fore and hind limbs, for mastication and for neck movements. The facial area became responsive considerably later, not until five days after birth, when closure of the eyes, and ear movements were obtained. Several days later the authors obtained in addition, movements of the upper lip. In agreement with Soltmann ('76) and Mills ('94, '95, '96) they found considerable individual variability as well as variability according to the different breeds of dogs.

Cat and dog as seen from the experiments of the various investigators exhibit the striking phenomenon that the limb areas considerably precede the facial area in their response to electrical stimulation, and that (according to Soltmann, Ferrier, Paneth, Michailow, v. Bechterew, Weed and Langworthy) the fore limb area precedes the hind limb area. Comparison with conditions found in the adult monotremes, marsupials and primitive representatives of the placentals moreover evidences the fact that, as regards the cortical motor representation, the fore limbs, presumably in functional adaptation, precede the hind limbs not only in the development of the individual but likewise in phylogeny. However, the great delay in the response from the hind limb and facial areas in the cat (Weed and Langworthy) as compared with the dog, is rather astonishing in view of the fact that cats in their general development during postnatal life make quicker progress than dogs (compare Mills on the psychic development of young animals, 1895, '96, p. 21). Renewed investigations with modification of the technique (e.g., stimulation of the animals without anesthesia) may yet lessen the unaccounted great difference between cats and dogs.

From the investigations by Fritsch and Hitzig (1870), Ferrier ('73, '74, '80, '86), Hitzig ('73, '74, '04), Luciani and Tamburini ('78, '83), Rosenbach and Bechterew ('83), Paneth ('85), Bechterew ('86/87, '87, 1911), Exner and Paneth ('87), Herrick and Tight ('90), Mann ('96), Mills ('96), Weed and Langworthy ('26), Langworthy ('27), etc. and from our own (Huber and Smith, unpublished) it becomes evident that the motor cortex in carnivores, especially cat and dog, has evolved further than in representatives of the above discussed orders of placentals. The readily responsive facial area appears to be more clearly

separated from the fore limb area (fig. 17b). Contraction of the facialis musculature is prevailingly contralateral, but to a certain extent also bilateral. Within the facial area, those muscles (fig. 11) which move the long mystacial tactile vibrissae (*M. naso-labialis* and *M. maxillo-naso-labialis*) are the most responsive ones, especially in the cat (see further chapter VI). Portions of the *M. orbicularis oculi* contract synergetically with the *M. naso-labialis*. The two muscles constitute a morphological and functional unit, and the cortical center for this genetic muscle group has evidently not received a further clear subdivision.

6. Primates. A far greater variety of the Primates has been investigated than of any other order of the placentals. It was, indeed, of great importance that these investigations should cover the main groups of the Primates in order, on the one hand, to link the findings in the lower representatives of this order with those of primitive types of other placentalian orders, and, on the other hand, to get, through comparative study of the catarrhine monkeys and apes, a key for the understanding of the complex conditions of the human motor cortex.

While many important general questions on the primate motor cortex have been intensively studied by a large series of investigators, our knowledge concerning the representation of the facial area in the motor cortex of the primates is very incomplete and in part contradictory. It is not at all correlated with the data from the extensive studies on the facialis musculature of this order (chapter VII).

A. Prosimiae (Tarsioidea and Lemuroidea).

Tarsius has not yet been subjected to experimentation, but there are records of observations on a number of the *Lemuroidea* by Elliot Smith and May (1904), Völsch ('06), C. Vogt ('06), C. and O. Vogt (1906/07) and Mott and Halliburton ('08).

In the brain of the Lemuroidea (fig. 18a) distinct responsive areas for the head, trunk, tail and both extremities were mapped out. From the facial area, movements of the *M. orbicularis oculi* and the musculature of the ears and snout were obtained. None of the investigators referred to vibrissae movements, which in the lemur should be expected to be an outstanding phenomenon (compare chapter VII). Easily obtainable contralateral ear movements were reported (C. and O. Vogt; Mott and Halliburton). This is in agreement with the fact that in the lemurs the ear musculature is well developed and differentiated (Ruge, Huber) corresponding to the great rôle which hearing, with the necessary adjusting mechanisms of the outer ear, plays in the nocturnal life of the animals. The closure of the eye was found prevailingly contralateral, while the snout musculature gave contralateral and bilateral response (C. and O. Vogt, p. 404). The Vogts emphasize the more caudal position of the area for closure of the eyes as being in striking contrast to the more oral position of the same area in the Simian cortex (p. 397, 406).

B. Simiae:

1. Platyrrhines.

a) Family Hapalidae (Marmosets). Investigations on representatives of this family were undertaken by C. and O. Vogt (1906/07), and Mott, Schuster and Halliburton (1910).

In agreement with the lowly position of the marmosets, their little or unfurrowed brain has no *sulcus centralis* which in the higher simians demarcates so clearly the motor area in front from the sensory area behind. However, the responsive motor cortex (fig. 18b) shows a topographic relation similar to that in the monkeys with a well defined *sulcus*

centralis Rolandi (figs. 18c—e). Responsive areas for the trunk, tail, upper and lower extremities and head have been mapped out. Mott, Schuster and Halliburton emphasize the large extension of the head area, including the facial field, which could be further subdivided and gave a more ready response than the fore and hind leg areas. In contrast to their previous investigation on the lemur (Mott and Halliburton, 1908) the authors did not obtain response from the ear musculature in the marmoset. Neither did C. and O. Vogt record ear movements. However, this negative result must not be considered final. It should rather be expected that a more elaborate investigation of the facial area will give ear movements, since the marmosets possess a well developed and fully functioning, though not highly differentiated ear musculature (chapter VII).

b) Family Cebidae. C. and O. Vogt (1906/07) seem to be the only authors who have experimented on representatives of this family—on *Nyctipithecus* (*Aotus*), *Pithecia*, *Cebus*, *Alouatta* and *Ateles* (fig. 18c). These important investigations of the Vogts bring, however, only scanty contributions to the exact knowledge of the facial area. It should be expected that a further elaboration of this area would take place in the "ascending scale of platyrrhines," paralleling the evolution of the facialis musculature. In the higher platyrrhines the fuller use of the more elaborate muscles of the face proper (mimetic musculature) is in striking contrast with the prevailing use of the musculature of the ear and snout and the specialized vibrissae moving facial muscles in the lower platyrrhines and prosimians (chapter VII).

2. *Catarrhines.* The number of the investigators who have carried out stimulation and ablation experiments and histological studies on the motor cortex of catarrhines is large. Since the problems hereby involved become more manifold and more complex in the "ascending scale of the catarrhines" the widely scattered literature on this subject has grown very extensive. The author has dealt more fully with this literature in another paper *A Phylogenetic Aspect of the Motor Cortex and the Cortico-Spinal Tract in Mammals, with Emphasis on the Facial Area* (in manuscript), while here only brief reference is made to it.

a) Lower Catarrhine Monkeys (Cercopithecidae). Hitzig (1874) was largely correct in his findings after exploration and delineation of the motor cortex of his only macaque. He clearly demonstrated and emphasized the fact that the electrically responsive area does not extend behind the *sulcus centralis Rolandi.* Ferrier (1874, '75, '80/86) claimed a much more extensive area including the postcentral gyrus, with additional areas scattered all over the outer surface of the cortex and even an area on the lower surface of the temporal lobe. A series of investigators (Horsley and Schäfer, 1884, '89; Schäfer, '87; Beevor and Horsley, '87, '94; Munk, '90, '92, '96, '03; v. Bechterew, '98, '99; Probst, '03; Rothmann, '04, '05, '07; E. Weber, 1906, and others) subsequently investigated the motor cortex of lower catarrhines. Partly influenced by Ferrier's inaccurate findings these authors mapped out the motor area in an extension far greater than actually exists, always including the postcentral gyrus in the electrically responsive area.

Then followed important contributions by various investigators (Sherrington and Grünbaum, 1901/02, '04; Brodmann, 1904, '05; O. Vogt, '06; Sherrington, '06; Sherrington and Roaf, '06; C. and O. Vogt, '06/07; Jolly and Simpson, '07), which indirectly (Sherrington and Grünbaum, '01/02, '04) or directly led to a more correct

delimitation of the motor areas in the lower catarrhines.

Yet for a long time it was disputed whether the postcentral gyrus had to be included in the electrically excitable motor cortex (compare controversies between Lewandowsky and Simons, 1909, '13, against Rothmann, '04, '05, '07, '12). As regards the precentral gyrus of the lower catarrhines (fig. 18d), the numerous experiments by many investigators including ourselves (Huber and Smith: on the macaque), agree in that response is readily and consistently obtained and the movements elicited are quite elaborate though not as elaborate as found in the anthropoid apes.

b) Gibbons (Hylobates and Symphalangus). C. and O. Vogt (1906/07), shortly refer to a stimulation experiment on *Symphalangus* by Brodmann. A fuller experimental and histological investigation on a second gibbon was made by Mott, Schuster and Sherrington (1911). In contrast to the lower catarrhines, the head area in the gibbon appeared relatively small in comparison with the extremity areas. Among these the arm area showed a striking increase in size, obviously in correlation with the deliberate use of the upper extremities in the brachiating habits of the gibbon.

c) Great Anthropoid Apes (Orang-Utan, Chimpanzee and Gorilla). It was not until 1891 that for the first time a representative of the great anthropoid apes, an orang, was subjected to experimentation by Beevor and Horsley. This was a step further in the study of the primate cortex and towards our knowledge of the motor functions of the human brain. This study was followed by the extensive stimulation and ablation experiments by Sherrington and his co-workers (Grünbaum and Sherrington, 1901/02, '04; Roaf and Sherrington, '06; Brown and Sherrington, '12, '13; Brown, '14; Leyton and Sherrington, '17). The last publication sums up the results and draws the conclusions from experiments on 3 orangs, 22 chimpanzees and 3 gorillas. An additional short account of the stimulation of an orang is included in C. and O. Vogt's work (1906/07).

The motor area of the anthropoid brain (fig. 18e), as compared with that of the gibbon and the lower catarrhines, was found to have grown in absolute extent, while other areas belonging to the so-called "silent" fields have increased still more. This vast expansion of unexcitable, richly convoluted fields is indeed among the most outstanding features of the highly organized neo-pallium of the anthropoid brain. Within the excitable motor area of the anthropoid brain, the areas representing the various parts of the body are arranged as in the lower catarrhines and higher platyrrhines. However, according to all investigators, more elaborate and very numerous movements from small subdivisions of the motor cortex can be obtained in the anthropoid brain. Thus we see in the "ascending scale of the primates" that the motor cortex evolves by individualization of emerging smaller areas within the principal motor area.

The three great anthropoid apes seem to resemble each other closely in regard to the motor cortex. But there are great individual variations and differences in the smaller details of localization of the right and left motor cortex of the same animal. In the orang, the facial area was found more extensive in relation to the rest of the motor area, being considerably longer from above down than in the chimpanzee and gorilla (Sherrington, 1906, p. 276; Leyton and Sherrington, 1917, p. 219). But apart from this distinction, there seemed no clear difference between the

motor area of the three types of the big anthropoid apes (Leyton and Sherrington, 1917, p. 219). That the motor cortex of the orang would differ, at least to some extent, from that of the chimpanzee and the gorilla could be expected in view of the fact that in the other organ systems the orang-utan departs widely from his anthropoid cousins, the chimpanzee and gorilla, who stay closely together. This has been found most striking in a close comparison of the mimetic musculature of the three types (Ruge, 1887; Huber, see figures of chapter VII). Renewed, comparative studies on the motor cortex of the three great anthropoid apes may possibly bring out further differences.

The comparative anatomical investigations on the catarrhine monkeys and the apes were of great significance in regard to the cortical representation of the mimetic musculature of man. In catarrhine monkeys and also in anthropoid apes, the mimetic musculature not only of the upper but also of the lower part of the face, especially of the lips, has been reported to be in part bilaterally represented in the motor cortex (compare e. g., Beevor and Horsley, 1894, on the macaque; 1891, on the orang). Such bilateral movements of the lip musculature in the orang have not been confirmed by the subsequent investigators. Contrary to Beevor and Horsley, Sherrington and his co-workers found that in the anthropoid apes bilateral representation of the mimetic musculature is restricted to and even accentuated in the muscles of the upper region of the face, i. e., the *M. orbicularis oculi*, *Mm. depressor* and *corrugator supercilii* and *M. frontalis*, but most noticeably in the *M. orbicularis oculi* (Grünbaum and Sherrington, 1904; Leyton and Sherrington, 1917). In this respect the great anthropoid apes thus resemble man closely, in whom, as seen from clinical cases and physiological observations, the mimetic muscles of the upper part of the face are evidently bilaterally represented.

d) *Man.* In order to make the study of the primate motor cortex complete, systematic experimental investigations on the motor cortex of man (fig. 19), in addition to the occasional clinical observations and the numerous data from brain pathology, were a prerequisite. Fortunately such data have been obtained through the efforts of a series of surgeons and neurologists (Krause, 1904, '05; Mills and Frazier, 1905; Cushing, '09; van Valkenburg, '12, *et alii*). For obvious reasons these experimental data from man cannot be as complete as those made during experiments on animals. Important is the fact that the results so far obtained, including those regarding the facial area, closely correspond with the results from the numerous and manifold experiments on the big anthropoid apes. This is in accord with the studies on the cyto-architecture of the anthropoid and the human cortex (Campbell, 1905; Brodmann, '09; v. Economo and Koskinas, '25).

In conclusion to this chapter the author suggests that special investigations on the facial area of the motor cortex should be undertaken with a broad knowledge of the facialis musculature with its manifold development and functional differentiation in the various mammalian groups.

FIG. 15. THE BRAIN OF ORNITHORHYNCHUS, WITH THE ELECTRICALLY RESPONSIVE MOTOR AREAS MAPPED OUT ON THE UNFURROWED CEREBRAL CORTEX

(According to experiments by Martin (1898/99).) Already in this archaic mammal the facialis field appears to be well represented in the motor cortex. From a large ill-defined area on the anterior half of the cortex, movements of the facialis musculature and of the fore limbs were obtained. Here facial and fore limb areas coincide in part, while a smaller area further back gave response of the facialis musculature only. No response of the hind limbs or tail was obtained.

FIG. 16. THE FORE BRAIN OF DIDELPHYS MARSUPIALIS (OPOSSUM) TO SHOW THE RELATION OF THE FACIAL AREA TO THE OTHER ELECTRICALLY RESPONSIVE AREAS OF THE CEREBRAL MOTOR CORTEX (MODIFIED AFTER WEED AND LANGWORTHY, 1925, AND FURTHER AUTHORS)

The main electrically responsive areas are grouped around the orbital sulcus. There facial and fore-limb areas overlap in part. Stimulation of the facial area at the lower end of the orbital sulcus also produces response of those facial muscles which move the facial tactile vibrissae (compare Huber and Smith), an outstanding phenomenon in stimulation of the opossum's cortex. Some investigators moreover reported hind limb and tail movements upon electrical stimulation of areas situated posterior to the fore-limb area. This response is, however, not regularly obtained, and has been disputed by more recent investigators.
(Note that facial and masticatory areas are closely associated.)

FIG. 17. THE FORE BRAIN OF THE CAT WITH THE ELECTRICALLY RESPONSIVE AREAS

a. New-born kitten (after Weed and Langworthy, 1926). The only response obtained at this age is from the fore limb area, which is situated in the same location as in the adult cat.
b. Adult cat (after Weed and Langworthy, and after observations by Huber and Smith). The electrically responsive areas are grouped around the *sulcus cruciatus*. From the well defined facial area at the lower end of this sulcus also movements of the facial tactile vibrissae, particularly of the mystacial vibrissae, are easily and regularly obtained. These movements are effected by contraction of the *M. naso-labialis* and *M. maxillo-naso-labialis*, as evidenced by exposing these muscles during the stimulation experiments (Huber and Smith).
(Note that facial and masticatory areas are closely associated.)

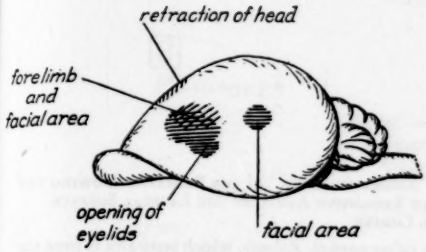


Fig. 15

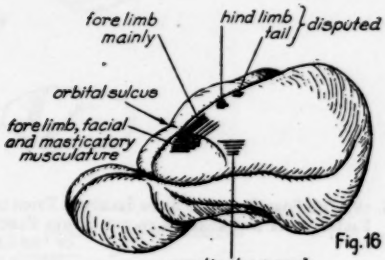


Fig. 16

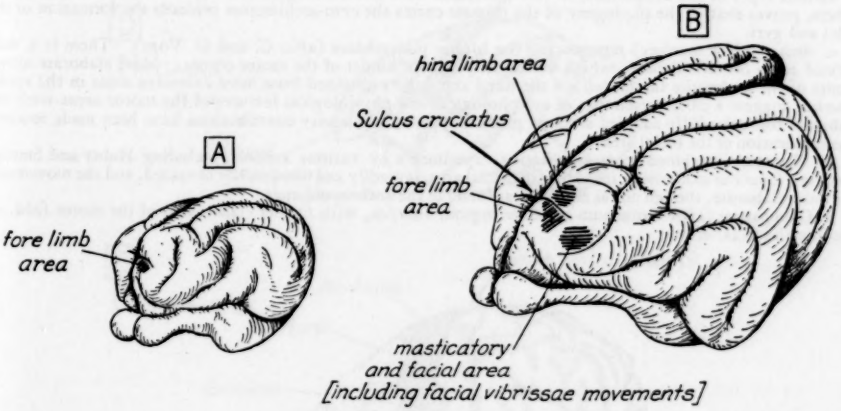


Fig. 17

FIG. 18. THE FORE BRAIN OF SOME SELECTED TYPES IN THE "ASCENDING SCALE" OF THE PRIMATES, SHOWING THE FACIAL AREA IN RELATION TO THE OTHER ELECTRICALLY RESPONSIVE AREAS ON THE LATERAL SURFACE OF THE CEREBRAL CORTEX

The motor field in the primates is a strip anterior to the *sulcus centralis Rolandi*, which separates it from the sensory field behind. Dorsally the motor area extends over on the medial surface of the hemisphere, and in the primates with a convoluted cortex it dips into the corresponding sulci. This increase of the motor field is very considerable in the richly convoluted cortex of the higher primates (compare *e*). The facial area is part of the "head area," which is situated at the lower end of the motor field. In addition to the facial area the "head area" includes subdivisions representing the masticatory muscles, the musculature of the tongue, larynx and vocal cord. Facial and masticatory areas are closely associated.

a. Lemur as a representative of the Prosimians (after C. and O. Vogt, 1906/07). The short furrow foreshadowing the *sulcus centralis Rolandi* demarcates the motor area in front from the sensory area behind.

b. *Callithrix* (marmoset) representing the lower platyrrhine monkeys (after C. and O. Vogt). In the unfurrowed brain of the Hapalidae the electrically responsive motor field shows the same topographic relations as in the monkeys which possess a well defined *sulcus centralis Rolandi*. This fact, together with the findings in various types of the Prosimians, in full agreement with the histological findings of Brodmann (1909) and others, proves that in the phylogeny of the primate cortex the cyto-architecture preceeds the formation of the sulci and gyri.

c. *Ateles* (spider monkey) representing the higher platyrrhines (after C. and O. Vogt). There is a well defined *sulcus centralis Rolandi*, which marks the posterior border of the motor cortex. More elaborate movements of the prehensile tactile tail, of the hand and fingers obtained from more extensive areas in the spider monkey suggest a close correlation of morphological and physiological features of the motor areas with the habits of this splendidly adapted arboreal primate type. Only scanty contributions have been made towards the exploration of the facial area.

d. Macaque (combined from stimulation experiments by various authors, including Huber and Smith). Response from the motor field, including the facial area, is readily and consistently obtained, and the movements are quite elaborate, though not as elaborate as found in the anthropoid apes.

e. Chimpanzee (after Grünbaum and Sherrington, 1901/02, with further elaboration of the motor field, including the facial area.

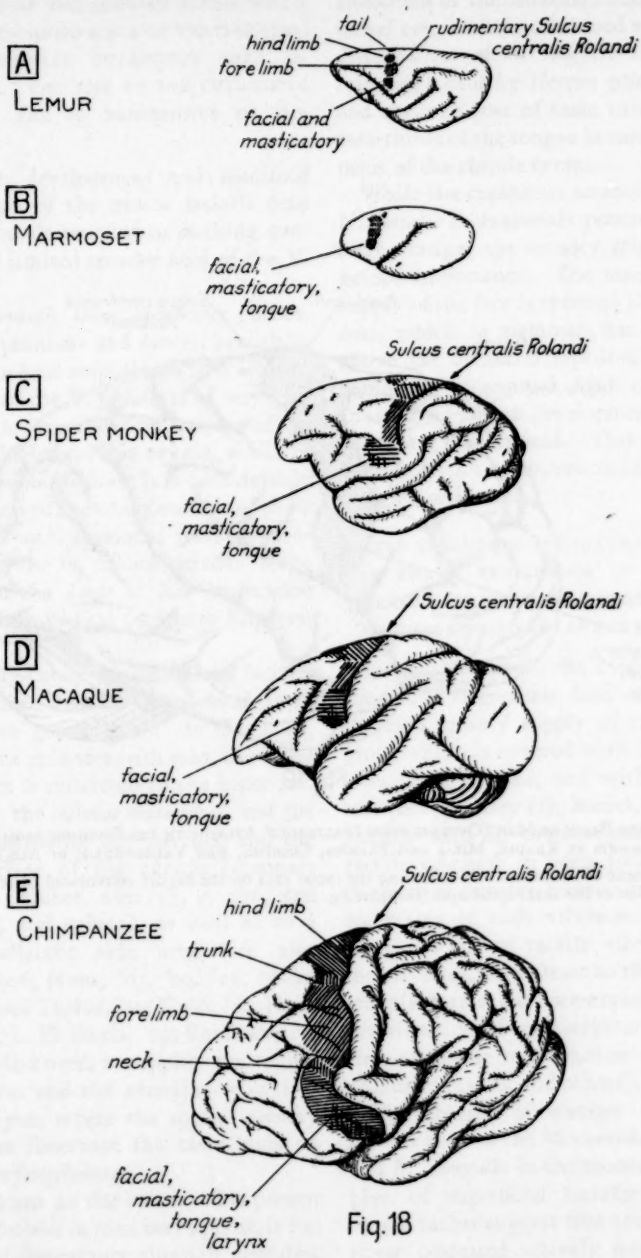

A
LEMUR
tail
rudimentary Sulcus centralis Rolandi
hind limb
fore limb
facial and masticatory
B
MARMOSET
facial, masticatory, tongue
C
SPIDER MONKEY
Sulcus centralis Rolandi
facial, masticatory, tongue
D
MACAQUE
Sulcus centralis Rolandi
facial, masticatory, tongue
E
CHIMPANZEE
Sulcus centralis Rolandi
hind limb
trunk
fore limb
neck
facial, masticatory, tongue, larynx

Fig. 18

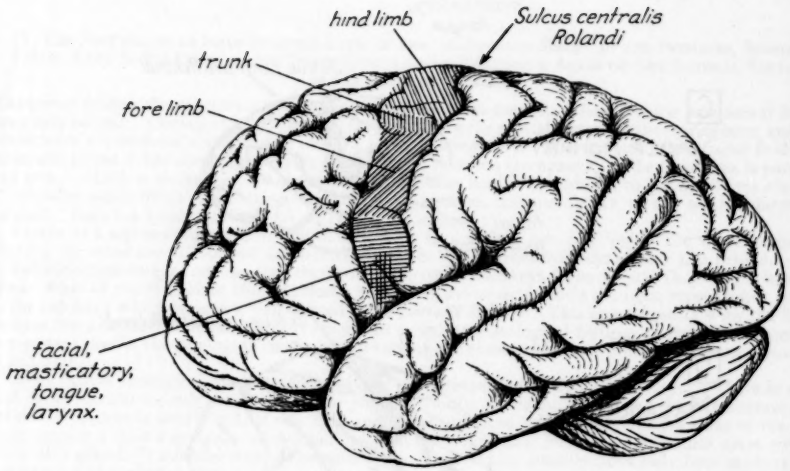


Fig. 19

FIG. 19. THE FORE BRAIN OF MAN (OUTLINE FROM SPALTEHOLZ' ATLAS WITH THE FINDINGS FROM STIMULATION EXPERIMENTS BY KRAUSE, MILLS AND FRAZIER, CUSHING, VAN VALKENBURG, ET ALII)

The arrangement of the motor field including the facial area on the highly convoluted cortex closely corresponds with that of the anthropoid apes (compare fig. 18c).

IV. DECLINE OF THE SENSORY FACIAL FIELD IN THE ASCENDING SCALE OF VERTEBRATES, WITH VESTIGIAL CUTANEOUS AREA IN MAMMALS. THE RISE OF THE CUTANEOUS FIELD OF THE N. TRIGEMINUS IN THE MAMMALS

The high development and manifold specialization of the motor facialis field of the mammals remains in striking contrast to the limited sensory field of the *N. facialis*.

In the *aquatic lower vertebrates* (fishes, aquatic amphibians and larval, branchial stages of the land amphibians) the sensory component of the *N. facialis* is of very considerable size, especially on account of the supply to the lateral-line organs, while in the adult *land amphibians* it is considerably reduced through the complete loss of these organs. In such a reduced state the sensory field of the *N. facialis* persists in the *reptiles*. In the *birds* it has undergone even further reduction (compare Kappers, 1910).

The reduced state of the sensory facialis field was taken over by the *mammals* from the reptilian ground plan. In mammals, including the primates with man, the facial sensory area is restricted to the inner ear, middle ear, the *cellulae mastoideae*, and the outer ear including the ear tube and the convex surface of the auricle (compare Boas, 1912; Huber, 1922/23, p. 376, and 1925, figs., and others), as well as to a variable adjacent skin area (see also Donath, 1906; Hunt, '07, '09, '15; Mills, '10; Clark and Taylor, '10; Kidd, '14; H. T. Davis, '14; L. E. Davis, '23; Reinhart '19, *et alii*). Moreover, it supplies the region of the fauces and the anterior two-thirds of the tongue, where the special sensory components innervate the taste buds on the *papillae fungiformes*.

Insignificant as the sensory component of the *N. facialis* in man may appear, it has its clinical importance through neuralgic affections of the internal, middle and external ear, at times combined with trophic disturbances of the auricle and its surroundings causing Herpes oticus (Hunt), and through loss of taste in the anterior two-thirds of the tongue in case of involvement of the chorda tympani.

While the cutaneous sensory area of the *N. facialis* in mammals persists thus as a mere vestige, the sensory trigeminal has gained importance. The main cutaneous supply of the face is through the *N. trigeminus*, which in mammals has evolved far above the ancestral reptilian plan. The cutaneous trigeminal field of mammals thus shows a high development similar to the motor facialis field. This may become evident from the discussion in the following two chapters.

V. THE EVOLUTION OF THE CUTANEOUS FIELD OF THE N. TRIGEMINUS IN THE MONOTREMES, CULMINATING IN THE ACQUISITION OF HIGH SENSITIVITY OF THE SNOUT

In the *Monotremes* the evolution of the cutaneous trigeminus field culminates in the rich sensory supply of the snout region, which is covered with a thin horny cuticule in *Echidna*, and with a smooth, soft (not leathery (!), Burrel, 1927, p. 10) flexible skin in *Ornithorhynchus*, bare of tactile vibrissae in both forms (fig. 20). A series of authors have searched in vain for traces of such vibrissae. This complete absence of tactile vibrissae in the monotremes, in contrast to the marsupials and placentals, has been explained through deterioration of such structures in connection with the modification of the snout (Maurer, Pocock and others).

The absence of vestiges of vibrissae-movers such as the *M. maxillo-naso-labialis* and *M. mentalis* in the monotreme ground plan of superficial facialis musculature would rather suggest that the monotremes never possessed actively movable tactile

vibrissae on the snout (Huber). Other facts,—above all the peculiar, distinct arrangement of the sensory nerves to the snout (Huber)—support this conclusion. The acquisition of high sensitivity over the whole snout evidently offered a similarly efficient or, in the case of *Ornithorhynchus*, an even more efficient mechanism than a snout beset with tactile vibrissae.

Ornithorhynchus is most instructive because in this animal the tactile sense of the snout ("oral sense") exceeds by far the olfactory sense (compare Elliot Smith, 1899), although the olfactory apparatus is by no means deteriorated. Jacobson's organ, part of this mechanism, is, indeed, very well developed in *Ornithorhynchus* (Symington, 1891; Elliot Smith, '95; Hines, 1929). Profound modifications of the snout including its skeleton have taken place in *Ornithorhynchus*. While in *Echidna* the prenasal processes of the intermaxillary bones jointly with the nasal bones form the roof of the nose (fig. 22e) in *Ornithorhynchus* (figs. 22a and c) these processes no longer meet in the middle line. The large nasal bones have expanded further rostralward, splitting the intermaxillary bones widely apart. The anterior end of the upper jaw is thus considerably broadened, and the large interspace between the intermaxillary bones is filled out with a cartilaginous plate. Over this queerly modified flattened end of the upper jaw the smooth, delicate, flexible skin is stretched, and the snout is thus transformed into a structure which indeed closely resembles a duck bill in shape (fig. 20). The end of the lower jaw is adjusted to this bill

From not less than fourteen distinct foramina on the upper and lower surface of both upper and lower jaw (figs. 22 a—d), large cutaneous branches of the trigeminal nerve emerge to supply the bill (figs. 21c).

These nerve branches have been carefully traced by the author to their exit from the foramina. This was all the more desirable as some of those foramina have been misinterpreted by paleontologists (O. Abel, 1922, p. 387, 391/392, and figs. 1 and 5; see also M. Weber, 1927/28, vol. II, p. 33/34, fig. 7) as vestigial alveoli for incisor and canine teeth. After exclusion of these teeth, the vestigial temporary molar teeth in the upper and lower jaw of *Ornithorhynchus* can now definitely be considered to be the last and only remnants of the monotreme dentition (Huber).

The rich supply of the snout with cutaneous branches of the *N. trigeminus* accounts for the enormous size of the sensory portion of this nerve (figs. 21a and b; see further Koelliker, 1901, p. 97; Elliot Smith, 1899, p. 320/321, 323/324, and fig. 1; Hines, 1929, fig. 46b) and the remarkable dimensions of the corresponding nucleus (see fig. 21b, *tuberculum quinti*, compare further Koelliker, 1901, p. 97).

The cutaneous trigeminal branches end in Pacinian-like tactile corpuscles located in groups of two to three at the base of peculiar epithelial structures, the "push-rods", which are in large numbers scattered over the entire muzzle (E. B. Poulton, '94; Wilson and Martin, '94). Through so rich a supply of special sense organs the duck-bill-shaped snout of *Ornithorhynchus* is turned into an extraordinarily sensitive organ fit for searching the weeds and mud of the Australian rivers for eggs and larvae of aquatic fauna, worms, small crustaceans (shrimps) and little bivalves, as has been described by a series of authors (compare e. g., Burrel, '27).

Also in *Echidna*, just as in *Ornithorhynchus*, the sense of smell together with tactile sense of the snout are the directing senses, while sight and hearing evidently play a minor rôle. But in *Echidna* in contrast to *Ornithorhynchus* the "oral sense" stays far behind the enormously developed olfactory sense (compare Elliot Smith, 1899). The cutaneous branches of the *N. trigeminus* are therefore of correspondingly smaller

dimensions (fig. 22f), and the foramina in the skull and lower jaw (fig. 22e) are of accordingly moderate size. The arrangement of these foramina is, however, the same as in *Ornithorhynchus*, and fundamentally different from the marsupio-placentalian plan (Huber).

Tactile sense of the snout ("oral sense") added to the olfactory sense, with which it is closely linked, must have given the monotremes a considerable advantage over their reptilian ancestors, which probably used the tongue as tactile organ, just as many modern reptiles do. The evolving "oral-sense", demanding its representation in higher cortical centers immediately adjacent to the rhinencephalon, was probably one of the important factors in the evolution of the monotreme neopallium.

Kappers was the first to refer to a probably existing correlation between "oral sense" and neopallium development (Kappers, 1908, p. 523; Kappers and Theunissen, 1908, p. 279/280; see further Edinger, 1911, vol. I, p. 383/384; Kappers, 1920/21, vol. I, p. 333, vol. II, p. 911, 1202).

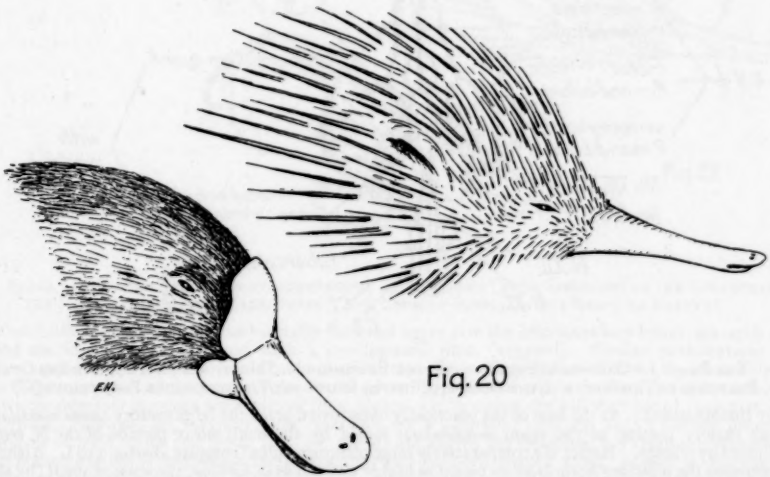


Fig. 20

FIG. 20. ECHIDNA, THE SPINY ANT-EATER WITH THE ELONGATED SNOUT COVERED WITH A SMOOTH, THIN, HORNY CUTICLE, AND ORNITHORHYNCHUS, WITH THE DUCK-BILL SHAPED SNOUT COVERED WITH A SMOOTH, SOFT, FLEXIBLE SKIN

At the base of the beak in the latter there are two shield-shaped, naked skin flaps, which protect the fur covered face above and below. Notice that in both monotremes there are no facial vibrissae, either on the modified snout or in the rest of the face. In *Ornithorhynchus* the orifice of the auditory meatus situated right behind the eye (compare fig. 5) is hidden in the thick fur. In *Echidna*, on the other hand, the anterior upper edge of the spoon-shaped ear cartilage (compare fig. 5) is seen as a slightly elevated structure over the surrounding skin, but there is no real external ear as in the case of the marsupials and placentals.

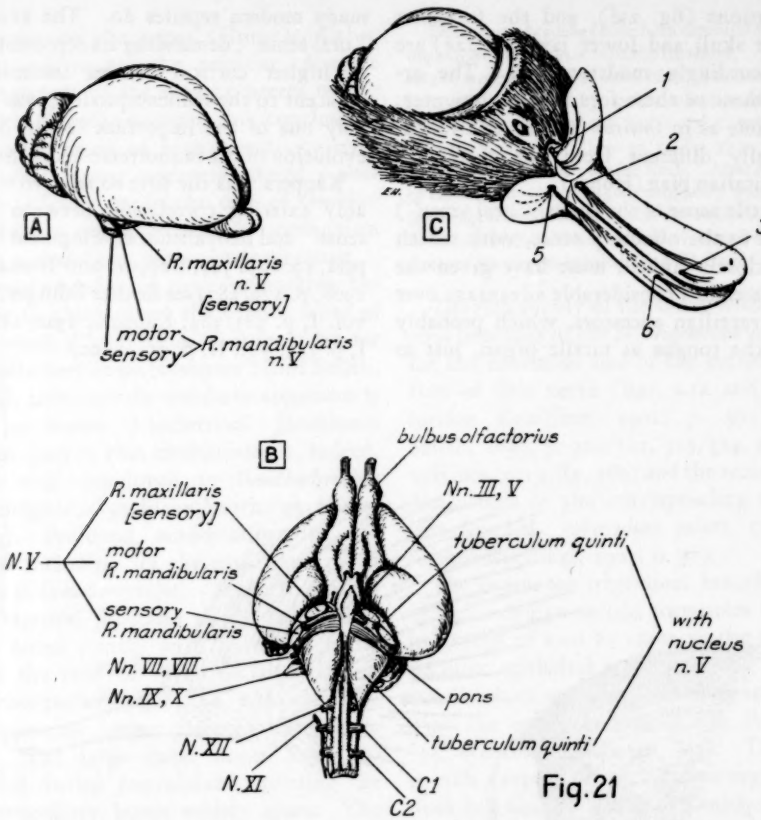


FIG. 21. THE BRAIN OF ORNITHORHYNCHUS WITH THE ENORMOUS N. TRIGEMINUS (A & B), AND THE CUTANEOUS BRANCHES OF THIS NERVE TO THE DUCK-BILL SHAPED SNOUT AND ITS SHIELD-LIKE PROJECTIONS (C)

a (by combination). At the base of the practically unfurrowed brain the large sensory *ramus maxillaris* and the large sensory portion of the *ramus mandibularis* joined by the small motor portion of the *N. trigeminus* are indicated by stumps. Notice the comparatively large olfactory bulbs (compare also fig. 21b). Although in *Ornithorhynchus* the olfactory brain is by no means as highly evolved as in *Echidna*, the sense of smell (by the way of the outer narial passages, as well as through the well developed Jacobson's organ, which opens into the oral cavity) probably plays an important rôle in the life of this animal.

b. Brain of *Ornithorhynchus* seen from below (slightly modified after Hines), showing the enormous size of the sensory portions of the *N. trigeminus* contrasted with the other cranial nerves as well as with the first and second spinal nerves. The enormous "*tuberculum quinti*" contains the correspondingly well developed *nucleus n. trigemini*. The sensory part of the *N. trigeminus* of *Ornithorhynchus* is, indeed, known to be larger than that of any other mammal.

c. (From a specimen of the National Museum collection, dissected by the author.) Large cutaneous branches of the *ramus maxillaris* and *ramus mandibularis n. trigemini* emerge from the skull to supply the bill and its shield-like projections. The rich sensory supply to the muzzle of *Ornithorhynchus* indicates that this is an exceedingly sensitive organ, ideally adapted for searching the mud and water plants of the Australian rivers for aquatic fauna, which constitute the food of *Ornithorhynchus*. According to Burrel (1928) *Ornithorhynchus* keeps eyes and ears tightly shut under water, feeling its way with the aid of the highly evolved "oral sense." *Echidna*, on the other hand, is largely guided by the sense of smell, although tactile sense of the snout, especially of the tip of the snout, plays an important rôle (compare legend to fig. 22).

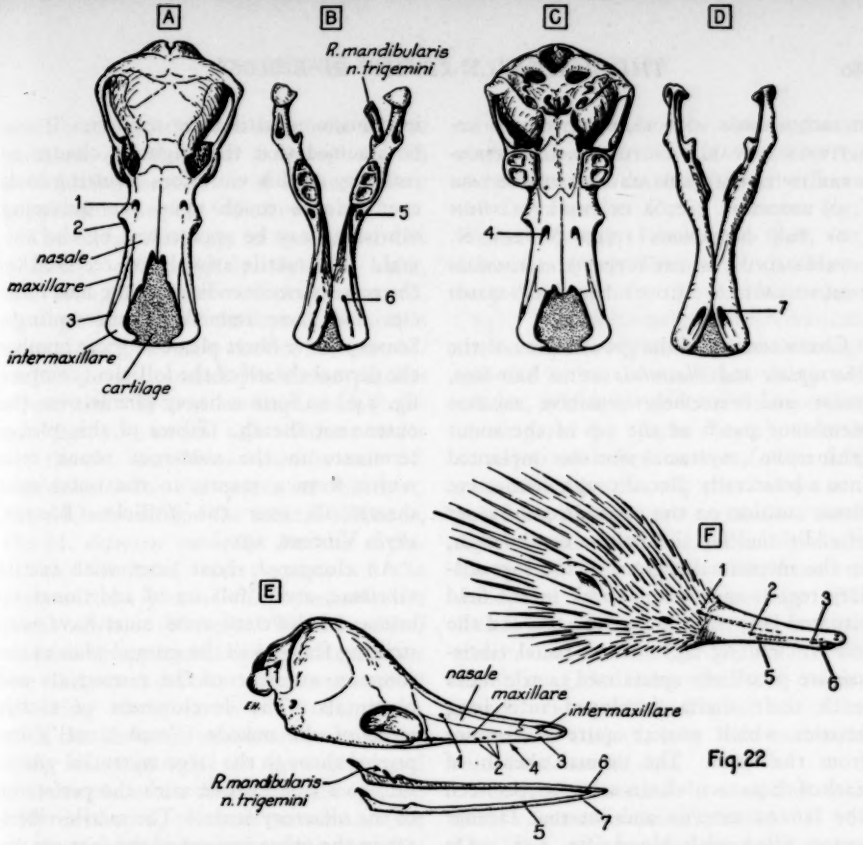


FIG. 22. SKULL AND LOWER JAW OF ORNITHORHYNCHUS AND ECHIDNA (FROM SPECIMENS OF THE COLLECTION OF THE NATIONAL MUSEUM, WASHINGTON), AND SENSORY SUPPLY TO THE SNOUT IN ECHIDNA

a–d. Ornithorhynchus. On the dorso-ventrally flattened upper jaw the intermaxillary bones are split wide apart, and the interspace is filled out with a cartilaginous plate (stippled). Similar modifications have taken place on the lower jaw. It should be emphasized that the cartilage indicated in the figures is only part of the cartilaginous plates of the jaws. A broad rim of cartilage outside and in front of the bony structures of the jaws considerably increases the width of these plates, which makes the bill very broad (compare e. g., Schimkewitsch, Lehrbuch der vergleichenden Anatomie der Wirbeltiere, 1910, fig. 146). On the upper and lower surfaces of both upper and lower jaw (fig. 22a–d) are shown the foramina (1–7) through which large cutaneous branches of the *N. trigeminus* emerge to supply the duck-bill shaped snout, as seen in the previous figure. The arrangement of these foramina is distinctly different from that of the marsupials and placentals; it is peculiar to the monotremes. Notice in figures 22b and c on the oral surface of upper and lower jaw the horny plates, which replace the vestigial, temporary molar teeth. These horny plates serve for crushing the shells of little bivalves which form an important part of the food of *Ornithorhynchus.*

e. Echidna, showing the same ground plan of trigeminal foramina on the skull and lower jaw as in *Ornithorhynchus.* There is a bilaterally placed foramen (1) on the upper surface of the nasal bone close to the naso-maxillary suture; three to four small bilateral foramina (2) laterally placed on the maxillary bone, evidently corresponding to the one large lateral foramen of *Ornithorhynchus;* one more, very small bilateral foramen (3) close to the tip of the elongated upper jaw in an exactly corresponding location as in *Ornithorhynchus,* at the junction of the maxillary bone with the intermaxillary bone; and one bilateral small foramen (4) on the lower (oral) surface of the maxilla in the same location as in *Ornithorhynchus.* Several little bilateral foramina are placed on the extremely slender mandible in the same locations as in *Ornithorhynchus,* one (5) considerably larger than the others, further back on the upper (oral) surface of the mandible, and two very small foramina close to the tip of the mandible on the inner (6) and outer surface (7) of this bone. Thus *Echidna* gets a considerable, though by no means as rich a supply of cutaneous trigeminal branches to the snout as *Ornithorhynchus.* The sensory part of the *N. trigeminus* in *Echidna* does not therefore reach such enormous dimensions as in *Ornithorhynchus.* Nevertheless the tactile sense of the snout plays an important rôle in Echidna as observed in the live animal. Notice in figure 22e that maxillary, intermaxillary and nasal bones form a rigid framework which encloses the nasal cartilage, in a similar way as in the reptilian plan. Because of the solid fusion of the individual bones in the skull of the adult Echidna the sutures are barely indicated in these places. The two mandibular bones however remain separate.

VI. ACQUISITION AND ELABORATION OF ACTIVELY MOVABLE TACTILE FACIAL VIBRISSAE IN THE MARSUPIALS AND PLACENTALS AN ESSENTIAL FACTOR IN THE EVOLUTION OF THE CUTANEOUS FIELD OF THE N. TRIGEMINUS, OF THE SUPERFICIAL FACIALIS MUSCULATURE, AND OF THE NEOPALLIUM

Characteristic of the ground plan of the *Marsupials* and *Placentals* are: a hair-free, moist and extremely sensitive mucous membrane patch at the tip of the snout (rhinarium), mystacial vibrissae implanted into a bilaterally placed tough connective tissue cushion on the upper lip, and a set of additional facial vibrissae on the chin, in the interramal region, in the supraciliary region and on the cheek in the field situated between the ear, the eye and the mouth cleft (fig. 23). These facial vibrissae are peculiarly specialized tactile hairs with their shafts developed into long bristles which project quite a distance from the head. The dermal sheath of each of these tactile hairs contains, between the lamina externa and interna, lacunar spaces filled with blood (fig. 24d). On account of these blood sinuses the tactile vibrissae have been termed "sinus hairs". Formation of such cavernous sinuses naturally increases the efficiency of these hairs as tactile organs. The slightest touch exerted upon the end of the long bristles transmitted through the stiff shaft to the springy cavernous hair sheath is thus extended over a larger sensitive area, and tactile impulses become intensified through this. The vibration of the loosely implanted hair shaft moreover prolongs the initial touch stimulus. Subliminal stimuli may through this be summated. Vibration of the hair shaft within the cavernous sheath of the follicle is undoubtedly of great importance. Many mammals, particularly small rodents, keep their heavily set, long mystacial vibrissae in continuous titillating motion. It can be assumed that the slightest change in intensity of this vibration, resulting from even minute touch upon the quivering vibrissae, may be appreciated by the animal. The tactile stimuli are received by the sensory nerve endings of the hair follicles and their immediate surroundings. Sensory nerve fibres pierce in great number the dermal sheath of the follicles (compare fig. 24e) to form a heavy plexus over the outer root sheath. Fibres of this plexus terminate in the numerous touch cells which form a mantle in the outer root sheath all over the follicle (Bonnet, 1878; Vincent, 1913).

An elongated snout beset with tactile vibrissae, and a full set of additional vibrissae in the cited areas must have been striking features in the ground plan of the common ancestor of the marsupials and placentals. The development of tactile sense of the muzzle ("oral sense") improved through the large mystacial vibrissae, goes side by side with the perfection of the olfactory sense. The tactile vibrissae in the other regions of the face are important additions. That the facial vibrissae are of vital importance as tactile organs, becomes evident through plain observations on the behavior of marsupials and placentals. This has also experimentally been demonstrated. Even when blinded through destruction of the visual area in the occipital lobe, opossums were able to move about and avoid obstacles by the use of the delicate touch pressure of the facial vibrissae (Rogers, 1924).

Most instructive are Vincent's experiments performed in connection with investigations on learning in the white rat (1912). This comprehensive behavior study gives clear evidence that the facial tactile vibrissae, particularly the mystacial vibrissae, are powerful organs of touch, which aid the animal in locomotion and

equilibration, in determining nearness or position of edges or corners, and in determining inequalities of surface. They supplement the poor vision of the rat.

The facial vibrissae, in contrast to the ordinary, only slightly sensitive hairs, are brought under voluntary control, through portions of the superficial facialis musculature, which have become attached to the connective tissue patches where the vibrissae are implanted (compare figs. 7, 9, 11 and 24). These muscles are the *M. maxillo-naso-labialis* and *M. naso-labialis* for the mystacial vibrissae, the *M. mentalis* for the mental vibrissae, the *M. depressor supercillii* for the supraorbital vibrissae, and portions of the platysma and *sphincter colli profundus* for the genal vibrissae (Huber). With the aid of this muscle apparatus the animals can move the vibrissae in different directions in order to bring them more freely in touch with the obstacles which are encountered along the trail. In the marsupials and in those placentals where the vibrissae are fully developed, vibrissae movements are an outstanding phenomenon in stimulation experiments on the facial area of the motor cortex. From a study of the findings of former authors one becomes aware that vibrissae movements were often believed to be a phenomenon occurring independently of the contraction of the facialis musculature. By exposing the superficial facialis musculature in opossum, cat and dog during the stimulation experiments it could be definitely proven that the vibrissae movements are indeed effected through contraction of the above mentioned muscles (Huber and Smith).

It is illuminating to view the different orders and suborders of marsupials and placentals in regard to the occurrence, distribution and manifold modifications of the facial tactile vibrissae. Scattered references to the distribution of the facial vibrissae are found in the older and newer zoological literature. Noteworthy are the publications on this subject by Bonnet (1878), Haacke ('90), Maurer ('95), Frédéric (1905), Friedenthal ('08, '11), Schwalbe ('11), Pocock ('14), Henneberg ('15), Müller ('19), Wood Jones ('23). Pocock investigated systematically the occurrence of facial vibrissae throughout the orders of mammals except the whales, which latter have however been investigated by Japha (1912), and by a series of other authors. The communication by Pocock may serve as a guide for further, more elaborate investigations on this field, which promises to be of great value also from the standpoint of systematic zoology. The author himself in his investigations on the facialis musculature has studied the distribution of the facial vibrissae. A brief sketch, whereby the findings of Pocock and others are utilized, may here summarize some fundamental data:

For most *Marsupials* a complete set of facial vibrissae is characteristic.

In the *polyprotodont marsupials* these vibrissae are generally found in a high state of development. A rare exception among this group is *Notoryctes typhlops*, a digging marsupial type adapted like *Talpa* among the placentalian insectivores. In *Notoryctes* the vibrissae are completely deteriorated on the elongated snout, which is covered with a rigid horn plate.

In the *diprotodont marsupials* (compare fig. 8) the facial vibrissae are usully shorter and less numerous than in the polyprotodont marsupials.

Among the *Placentals* in many *Insectivores*, *Bats*, most *Carnivores* (the bears exempt), in *Rodents* and in the *Prosimians* (compare next chapter on the Primates) the typical primitive distribution and development of facial vibrissae is found in full correspondence to that in the marsu-

pials. The other orders of the placentals show manifold modifications. Within the heterogeneous group of the "*Edentates*" the facial vibrissae are deteriorated in the anteaters (*Tamandua*, *Manis*, *Myrmecophaga*) and in the slow climbers (*Bradypus* and *Choloepus*), while in the armadillos they are retained, often hardly distinguishable from the ordinary hairs. Moderately long and fine facial vibrissae persist in many *Ungulates*, while they are aborted in other representatives of the ungulate stock, e. g., in the Rhinoceros and Hippopotamos. Scanty vibrissae vestiges are found on the proboscis of the *elephants*.

Most interesting are the modifications of the facial vibrissae in *mammals with aquatic adaptation*. Even some of the aquatic *fissipede carnivores* (e. g., the otters) show greatly enlarged mystacial vibrissae, while, on the other hand, the polar bear has the vibrissae reduced, just as the whole bear stock from which the polar bear sprang. The very broad, sensitive rhinarium characteristic of the bears, may here substitute for the mystacial vibrissae.

In the *Pinnipedes* the mystacial vibrissae are represented by long stiff bristles (compare fig. 24a), which are thicker than those of any other mammal. They have a characteristic arrangement in the different pinniped genera and species (Huber). A large bundle of nerve fibers from the *N. infraorbitalis* connects with the bulbs of these huge sinus hairs and with their immediate surroundings (fig. 24b). This makes the whiskers of the pinnipedes an effective mechanism for appreciation of slight changes in water pressure. The pinnipedes may thus avoid injuries to the guiding head and the following body while they swiftly swim about and boldly dive along rocky shore lines, or while they play tumultuously amidst irregularly shaped ice cakes in the far north.

In the group of *Sirenia*, slow marine mammals, on the other hand, the vibrissae on the strangely modified upper lips, i. e., the mystacial vibrissae, are short tough bristles, which aid the animals in grazing on the bottom of the sea.

In the *Whales*, the most highly specialized marine mammals, we find the most remarkable modifications of the facial vibrissae apparatus. For the whale, acquisition of a highly sensitive mechanism for appreciation of changes in water pressure, an apparatus with the same function as the lateral-line organs in fishes, was a prerequisite for successful adaptation to exclusively pelagic life. In this, as in so many other points, the two groups of living whales, the tooth whales and the whale-bone whales, have differentiated along separate lines.

The *whale-bone whales* (Mysticeti) possess a large number (up to over 130, according to M. Weber) of peculiarly modified mystacial and mental vibrissae (compare also fig. 25c). While the bristles of these tactile hairs are vestigial their hair sheaths persist, and the blood sinuses therein have reached further extension and elaboration. According to Japha every one of these tactile hairs is supplied with several hundred myelinated nerve fibers, with which tactile Pacinian-like corpuscles are connected. The occurrence of Pacinian corpuscles in connection with hairs is peculiar to the whales.

In the *toothed whales* (Odontoceti) vestiges of similarly modified mystacial vibrissae are found only during fetal life (fig. 25a). The functionally important tactile vibrissae apparatus is replaced presumably, according to the author's interpretation, by other mechanisms, the "melon" in all the toothed whales with the exception of the physeterids, and its corresponding structure, the "junk", and possibly the spermaceti cushion, in the aberrant odontocete group of the physeter-

ides. The "melon" is a peculiar accumulation of modified fatty tissue just in front of the blowhole (figs. 25b). It is richly supplied with cutaneous branches from the huge infraorbital nerve (fig. 25c), which leave the skull through as many as 6–9 separate bilateral foramina (fig. 25d) far apart from each other (Huber). The multiple emergence of these sensory nerves is evidently secondary, for there is just one large foramen for the *N. infraorbitalis* in archaic fossil whales among the extinct group of the zeuglodonts, as noticed in various museum specimens.

The modified tactile vibrissae apparatus in the whalebone whales, the "junk" and the spermaceti cushion in the physeterids, and the "melon" in the rest of the toothed whales, have been interpreted by the author as hydrostatic organs. Both the toothed whales and the whalebone whales are dependent on such a mechanism. Without it they could not possibly have become successfully adapted to exclusively pelagic life. The delicate sensory apparatus on the snout of the whalebone whales would naturally also assist these strangely specialized mammals in their pursuit of plankton (Japha), which they take in enormous quantities. Most of the toothed whales, on the other hand, which feed on larger animals like fishes and large cephalopods, or Orca, the fierce "killer", which feeds on mammals (seals, porpoises and even bigger whales), are guided in their food pursuit by vision. One exception to this is the aberrant, blinded *Platanista*, which lives in muddy rivers, mainly feeding on crustaceans (M. Weber). It would be important to learn whether the numerous sinus hair anlagen which have been reported to exist on the upper and lower jaws in Platanista fetuses (Weber, 1927/28, vol. II, p. 355), possibly develop into modified tactile organs similar to those of the whalebone whales.

It is through the *N. trigeminus* that all the tactile facial vibrissae receive their sensory innervation. The cutaneous branches of this nerve are, indeed, most abundant in the areas where the facial vibrissae are implanted, and we have good reason to assume that the various vibrissae groups determined the locations where individual cutaneous trigeminus branches should emerge from the skull (Huber).

There exist, naturally, modifications according to the construction of the skull, as in regard to the formation of the zygomatic arch, the bony frame of the orbit, the shape of the maxilla, etc. Moreover, the foramina may be duplicated or multiple. This seems to be characteristic for certain groups of the placentals, so that the arrangement of the trigeminal foramina might become of some systematic value. The individual variability, however, is great.

The established plan of distribution of these foramina for the respective cutaneous branches of the *N. trigeminus* in the lower primates, presumably determined by the arrangement of the facial vibrissae groups (see chapter VII), is retained throughout the ascending scale of primates, despite the deterioration of the vibrissae as tactile structures. Thus we find in man (fig. 26) in the same locations the *foramen infraorbitale* for the *N. infraorbitalis*, the *foramen supraorbitale* or *incisura supraorbitalis* for the *rami supraorbitalis* and *frontalis* of the ophthalmic division of the trigeminal nerve, the *foramen zygomatico-faciale* for the *N. zygomatico-facialis*, and the *foramen mentale* for the *N. mentalis*. Multiplication of these foramina are not uncommon variations and have often been referred to in the anatomical literature.

The studies on the facial vibrissae and their innervation lead to the conclusion that the evolution of the sensory field of the *N. trigeminus* in marsupials and

placentals is closely linked with the acquisition of these facial tactile vibrissae (Huber). And there is clear evidence that the elaboration of this important head protecting and guiding mechanism of tactile vibrissae, actively movable through facial muscles, was one of the causal factors in the evolution of the marsupio-placentalian ground-plan of the superficial facialis musculature (about other causal factors, see Huber, Morphol. Jahrb., 1922/23, p. 400).

Requiring sensory as well as motor representation in higher, cortical centers, the evolving facial tactile vibrissae apparatus of the common ancestors of the marsupials and placentals must thus also have played an influential rôle in the early stages of evolution of their neopallium (see also Kappers, 1908, 1920/21; Edinger, 1911; Wood Jones and Porteus, 1928, pp. 99, 167, and others).

(To be continued)

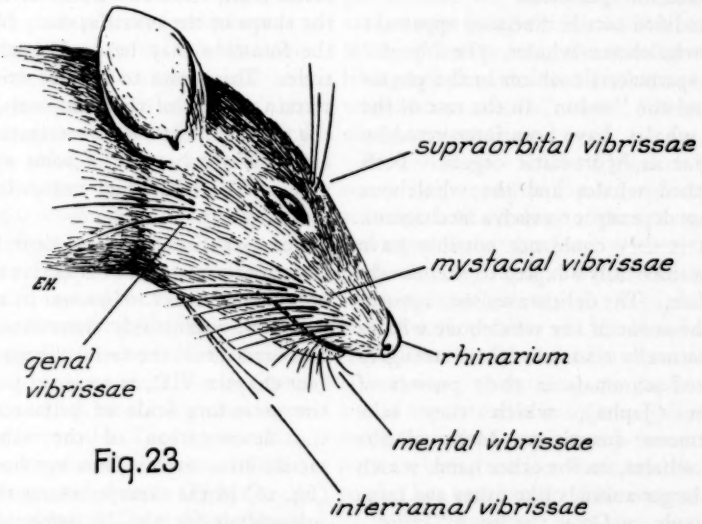


FIG. 23. SCHEME OF THE ARRANGEMENT OF THE FACIAL TACTILE VIBRISSAE WHICH ARE CHARACTERISTIC OF THE MARSUPIO-PLACENTALIAN GROUND PLAN

The facial vibrissae are arranged in definite groups (supraorbital, mystacial, mental, interramal and genal vibrissae). They receive their sensory supply from cutaneous branches of the *N. trigeminus*. Unlike the ordinary hairs these vibrissae (sinus hairs, compare further figs. 24c–e) are under voluntary control of facial muscles, which are inserted into the connective tissue patches into which the vibrissae are implanted, as shown in previous figures of chapter 1. (Compare figs. 7, 8, 9, 11.) Notice that in contrast to the monotremes, only the tip of the snout is naked in the marsupials and placentals. It forms the rhinarium, which is a moist, extremely sensitive mucous membrane patch. The rhinarium jointly with the mystacial and mental vibrissae serves the "oral sense" (tactile sense of the snout), which is closely associated with the olfactory sense. Yet the rhinarium is not only essential as a tactile structure, but owing to its moist and comparatively large sensitive surface it is of great assistance in quickly informing the animal about the direction of scent carried to the nose by the lightest wind. Also in this function it supplements the olfactory mechanism. The mystacial vibrissae and the rest of the facial vibrissae on the other hand form a vitally important protective mechanism. It is not astonishing that this should be best developed on the head, the guiding part of the body. Additional tactile structures, the carpal and tarsal vibrissae, likewise sinus hairs, and the guarding hairs of the fur serve as guiding mechanisms and belong to the marsupio-placentalian ground plan. While this primitive ground plan has been retained in a host of marsupials and in many primitive placentals, it has in other representatives of the placentals become modified and specialized along many lines.

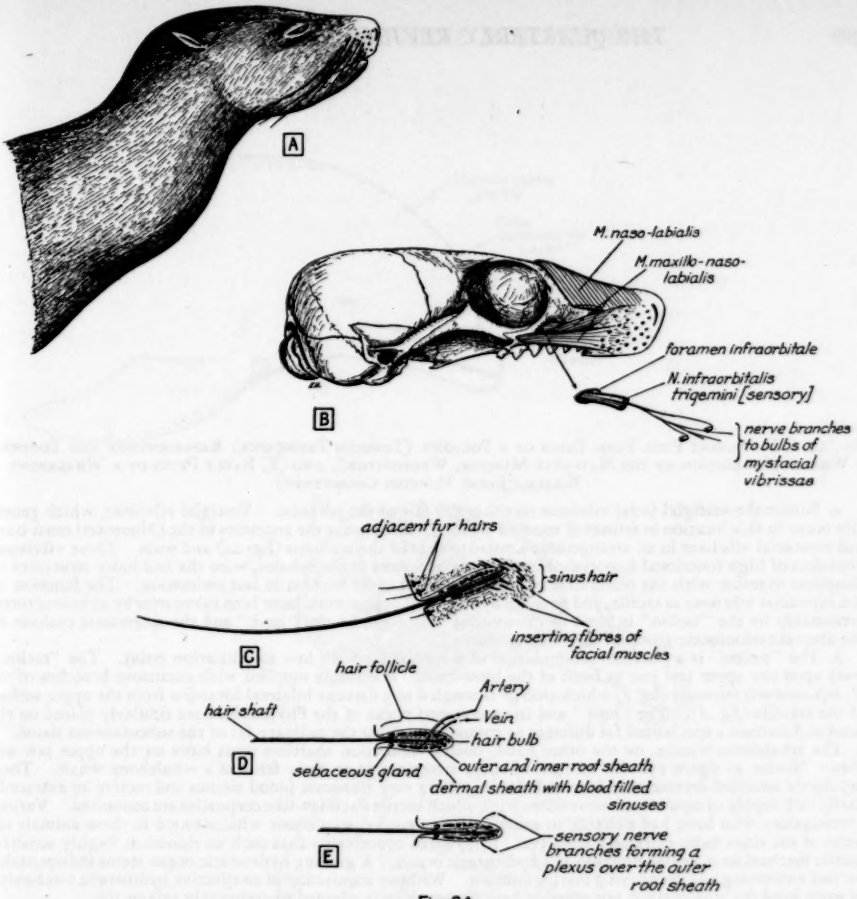


Fig. 24

FIG. 24 A AND B. SEA-LION (ZALOPHUS CALIFORNIANUS) OF THE JOHNS HOPKINS COLLECTION, SHOWING THE LONG, STIFF MYSTACIAL BRISTLES

Of all the mammals the sea-lions and seals possess the largest mystacial vibrissae. *b* shows the skull of a sea-lion with the soft parts of the snout. Bilaterally placed there is a tough connective tissue cushion into which the mystacial bristles (cut) are implanted. Facial muscles, the *M. maxillo-naso-labialis* and *M. naso-labialis*, insert into this cushion, and bundles of these muscles connect with the bulbs of the sinus hairs, which are thus put under voluntary muscular control. From the large infraorbital foramen emerges the unusually thick *N. infraorbitalis trigemini*. In the additional little figure a branch of this sensory nerve is shown with twigs terminating on the bulbs of the mysticial bristles and in their immediate surroundings. The highly sensitive mystacial vibrissae are of vital importance for the pinnipedes, as already emphasized in the text.

c–e. A schematic representation of the topography and structure of the sinus hair.

c, showing a sagittal section through the skin, with a sinus hair in situ, and 3 small adjacent fur hairs. The large shaft of the sinus hair projects a long distance above the surface of the skin, while the large follicle of the sinus hair is lodged deep in the subcutaneous tissue. A few striated muscle fibres of the facial musculature are seen inserting into the follicle.

d, showing a large artery entering the dermal sheath of the sinus hair. It leads into the elaborate blood sinuses of the follicle, while the accompanying vein drains these sinuses. The cavernous, blood-filled dermal sheath of the follicle thus forms a springy cushion, into which the root of the hair shaft, invested with the outer and inner root sheath, is implanted. At the neck of the hair follicle sebaceous glands drain into the follicle cavity. The secretion of these sebaceous glands oils the hair shaft and thus keeps the bristle elastic.

e, showing the sensory nerve supply to the sinus hair. Two cutaneous branches of the trigeminal nerve, composed of a large number of fibres, are seen entering the hair follicle. After having pierced the dermal sheath the nerve fibres spread out to form a dense plexus over the outer root sheath. Terminal fibres from this plexus connect with the "tactile cells of Merkel" lodged in the outer root sheath.

FIG. 25 A–D. ALMOST FULL TERM FETUS OF A PORPOISE (TURSIOPS TRUNCATUS) REPRESENTING THE TOOTHED WHALES (COLLECTION OF THE NATIONAL MUSEUM, WASHINGTON), AND (E) EARLY FETUS OF A WHALEBONE WHALE (JOHNS HOPKINS COLLECTION)

a. Notice the vestigial facial vibrissae on the upper jaw of the porpoise. Vestigial vibrissae, which generally occur in this location in fetuses of toothed whales, indicate that the ancestors of the Odontoceti must have had mystacial vibrissae in an arrangement similar to that of the sea-lions (fig. 24) and seals. These vibrissae, doubtless of high functional importance in the early ancestors of the whales, were the last hairy structures to disappear together with the other structures which might cause friction in fast swimming. The function of the mystacial vibrissae as tactile, and possibly hydrostatic, organs must have been taken over by new structures, presumably by the "melon" in most of the toothed whales, or by the "junk" and the spermaceti cushion in the aberrant odontocete group of the Physeteridae.

b. The "melon" is a peculiar accumulation of a special fat with low solidification point. The "melon" rests upon the upper jaw just in front of the blow-hole. It is richly supplied with cutaneous branches of the *N. infraorbitalis trigemini* (fig. *c*) which emerge through 6 to 9 distinct bilateral foramina from the upper surface of the maxilla (fig. *d*). The "junk" and the spermaceti organ of the Physeteridae are similarly placed on the head and contain a specialized fat different in composition from the ordinary fat of the subcutaneous tissue.

The whalebone whales, on the other hand, possess numerous, shaftless sinus hairs on the upper jaw and chin. Notice in figure 25e the anlagen of these structures in an early fetus of a whalebone whale. These peculiarly modified mystacial and mental vibrissae have very elaborate blood sinuses and receive an extraordinarily rich supply of myelinated nerve fibres with which tactile Pacinian-like corpuscles are connected. Various investigators who have had a chance to examine live, stranded whalebone whales found in these animals the areas of the sinus hairs extremely sensitive. It is indeed conceivable that such an elaborate, highly sensitive tactile mechanism may also function as a hydrostatic organ. A guiding hydrostatic organ seems indispensable for fast swimming and deep diving marine animals. Without acquisition of an effective hydrostatic mechanism of some kind the whales could not possibly have become ideally adapted to exclusively pelagic life.

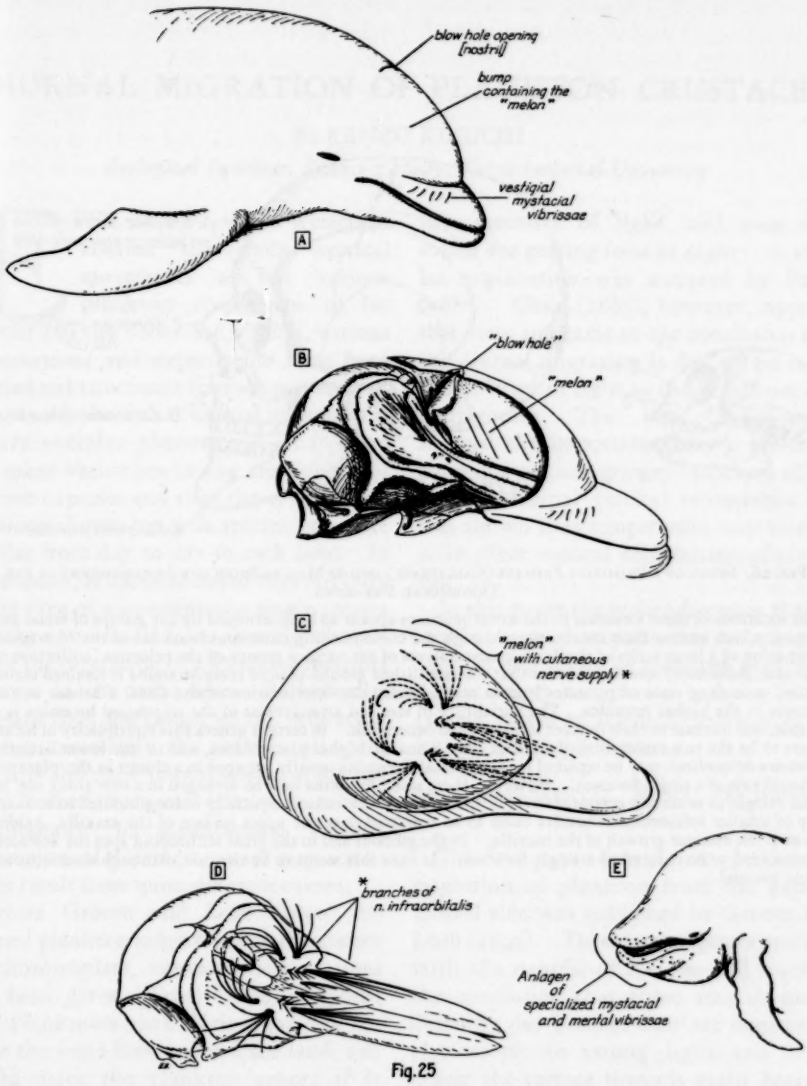

blow hole opening (nostril)
bump containing the "melon"
vestigial mystacial vibrissae
A
"blow hole"
"melon"
B
C
"melon" with cutaneous nerve supply *
D
* branches of n. infraorbitalis
E
Anlagen of specialized mystacial and mental vibrissae

Fig. 25

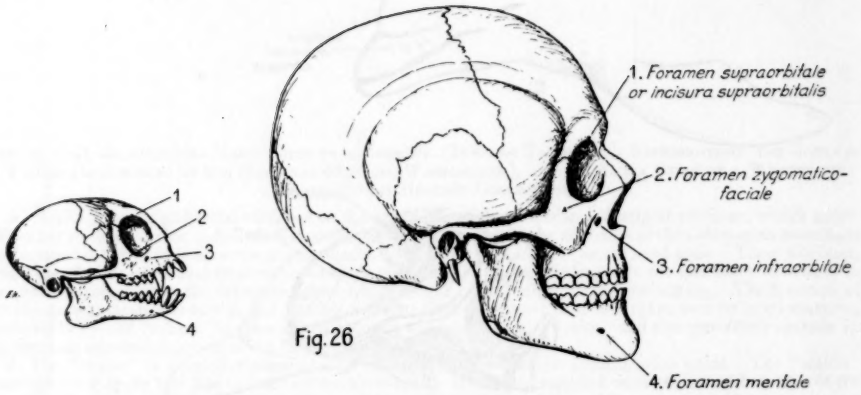


FIG. 26. SKULL OF A PRIMITIVE PRIMATE (CALLITHRIX) AND OF MAN TO SHOW THE ARRANGEMENT OF THE TRIGEMINAL FORAMINA

The locations of these foramina in the lower primates appear to be determined by the groups of facial tactile vibrissae, which receive their innervation through the corresponding cutaneous branches of the *N. trigeminus*. Examination of a large series of skulls of representatives of the various groups of the primates (collection of A. H. Schultz, Baltimore) revealed the fact that the established ground-plan of these foramina is retained throughout the "ascending scale of primates" up to man, despite the deterioration of the facial vibrissae as tactile structures in the higher primates. The variability in size and arrangement of the trigeminal foramina is considerable, and increase in their number is of common occurrence. In certain genera this multiplicity of foramina appears to be the rule rather than the exception. Thus in higher platyrrhines, and in the lower catarrhines the *foramen infraorbitale* may be replaced by 3, 4, 5 small foramina usually grouped in a cluster in the place where we should expect a single foramen. However, these small foramina may be arranged in a row along the infraorbital margin as in certain representatives of the baboons. In others, especially in long snouted baboons, the group of smaller infraorbital foramina came to be scattered over the upper surface of the maxilla, evidently because of the extreme growth of the maxilla. In the gibbons and in the great anthropoid apes the infraorbital foramina tend to be reduced to a single foramen. In man this seems to be the rule, although double foramina are not unusual.

DIURNAL MIGRATION OF PLANKTON CRUSTACEA

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EVER since Forel and Weismann studied the daily vertical movements of the various plankton crustaceans in lac Léman and the Boden See in 1874, various observations and experiments have been carried out to account for such migrations. The results show that diurnal migration is a very complex phenomenon, that there are great variations in the movements of different species and that the types of migrations shown by each species are quite similar from day to day in each lake. In a few cases, it has been noted that not only is the type of movement of a single species not the same in all lakes, but the character of the migration of a species sometimes changes in the same lake. Experiments indicate that the causes of the migration are not necessarily the same in all cases and it is therefore impossible to apply the facts learned from one species to others. Furthermore the simultaneous vertical movements of different species may sometimes result from quite different causes.

Before Groom and Loeb (1890) explained plankton migrations on the theory of phototropism, various interpretations had been given. Forel (1874) supposed that planktonts sank during the day because the wind blew toward the land, and would drive the plankton ashore if it remained near the surface, while in the night planktonts came nearer the surface because the wind blew from the shore. Weismann (1877) was of opinion that the crustaceans performed daily vertical movements because their eyes were adapted to a low intensity of light, and were thus suited for getting food at night. A similar explanation was accepted by Fuchs (1882). Chun (1887), however, opposed this view and came to the conclusion that the diurnal migration is due not so much to the effect of light as to the influence of temperature. The later observations showed the importance of the interrelations of light and gravity as factors affecting the diurnal vertical movements. It was shown that temperature may secondarily affect vertical distribution of plankton.

In this paper the writer discusses the observations and experiments relating to vertical migrations of plankton organisms and attempts to give an account of the present status of scientific knowledge relating to such phenomena.

THE EXPERIMENTAL STUDY OF DIURNAL MIGRATIONS

The first paper bearing on the diurnal migration of plankton from the experimental side was published by Groom and Loeb (1890). These investigators worked with the nauplii of *Balanus* and reached the conclusion that these animals move down by day because they are negatively phototropic to strong light and come nearer the surface towards night because they are positively phototropic to faint light. Loeb (1893) later found that *Daphnia*, *Polygordius* larvae, and *Temora longicornis* became positively phototropic when the water surrounding them was cool, but were negatively phototropic in warm

water. By adding sodium chloride to sea water, the same species of animals were shown to become positively phototropic and a decrease of salinity had the same influence as the warming of the water. Loeb further found (1904, 1906) that copepods, *Daphnia*, the nauplii of *Balanus*, and *Gammarus* were made positively phototropic by adding carbon dioxide or other acids. A general conclusion based on these experiments was given by Loeb in 1908. He states that as the temperature of surface water falls and CO_2 content increases toward night, positive phototropism is induced in animals, while in the morning, when the surface water is warmed by the sunlight and the CO_2 content decreases because of the photosynthetic activity of phytoplankton, animals become negatively phototropic. All these factors were affirmed to cause an animal to move down from the surface by day and come nearer the surface at night. In the daytime animals are believed to descend until they reach cold water, where they become positively phototropic. Loeb regarded gravity and the viscosity of water as additional factors influencing migration. He (1914) later added "the periodic changes in the internal chemical processes of the organism in relation to the phototropism" as another accessory factor. However, it is quite improbable that the actual daily changes in the temperature and carbon dioxide content of the water of a lake or of the open ocean are large enough to change phototropism from positive to negative or vice versa.

Bauer (1908) found that *Macropsis*, a mysid, showed a tendency to positive phototropism in horizontal rays, while it swam downward in the same intensity of light from above. This fact does not agree with Loeb's theory. Perhaps such behavior is due to a strong positive geotropism induced by light, as Dice (1914) has suggested.

Parker (1901) states that the females of the copepod, *Labiodocera aestiva*, swim down in the morning because they are negatively phototropic to strong intensities of light and move up in the evening because they are positively phototropic and negatively geotropic in weak light. He states that the females show more strongly marked negative geotropism than the males. The females are positively geotropic in water warmer than 26°C, though negatively geotropic in colder water. Parker further suggests that the males follow the females in their migrations because they are probably positively chemotropic to them.

The reversal of geotropism with the change of the intensity of light was first observed by Esterly (1907) in the female of *Cyclops albidus*. He found that the female of *Cyclops* is ordinarily positively geotropic, but after having been in light such animals tend to become negatively geotropic in darkness. He further states (1912) that sooner or later such an animal becomes again positively geotropic in the dark without any change in external conditions. He offers a possible explanation of diurnal migration based on the effect of light upon geotropism. The same phenomenon was observed by Harper (1907) in *Corethra* larvae, by McGinnis (1911) in *Branchippus serratus*, and by Dice (1914) in *Daphnia pulex*.

Dice (1914) studied the reactions of *Daphnia pulex* to various factors, such as light, gravity, temperature, chemicals, mechanical stimuli, locomotor activity of the organism, and age of individual with particular reference to vertical movements. He shows that an increase in temperature has a tendency to decrease the positive phototropism, while a decrease tends to make the animals more strongly positive.

At temperatures below 12°C. they are positive to all intensities of light. Increase of light intensity and high temperature cause a tendency to positive geotropism, while decrease in light intensity and low temperatures produce a tendency to negative geotropism. Dice came to the conclusion that the reversal of geotropism with the change of light intensity is a predominant cause in affecting the diurnal vertical movements of *Daphnia pulex*. He regarded phototropism as an accessory factor which determines the upper and lower limits of vertical distribution.

THE WORK OF ESTERLY

An important paper by Esterly (1919) deals with experiments on the phototropism and the geotropism of marine copepods and chaetognaths, with special reference to the diurnal migration. Two very important characters of *Acartia* were pointed out. First, Esterly showed that specimens obtained from the surface water react in different ways to light, gravity, and temperature than those obtained from deep water. The latter, however, react in all respects as do the animals from the surface water after they have been kept in a laboratory for a time. In the second place, he pointed out that there is a physiological rhythm in connection with the geotropism of species. This does not appear to be connected directly with external changes occurring at the time. Esterly observed that the animals are found largely toward the bottom of a glass tube when kept in the dark during the day. But from 6 p.m. to 8 p.m. there is a noteworthy increase of animals at the top, even if surrounding conditions are kept the same as before.

Esterly reached the general conclusion that each species has its own way of performing vertical movements and no general explanation of the diurnal migration can be given at present. It appears that changes in geotropism with changes in light intensity or in temperature are not general enough to be considered as of wide significance. The possible bearings of the experiments on the diurnal migration of each species are given in connection with the field observations made by Esterly in the San Diego Region, 1905 to 1911. The absence of the plankton copepods from the surface of the sea during the day may be explained by the fact that they are negatively phototropic to strong light. Esterly is quite positive that in *Acartia* the physiological rhythm of the animals ought to be considered as the primary cause affecting the upward movement in the evening. There is some evidence of a similar condition in *Calanus*. The field data show that these copepods leave the surface in the early part of the night. Positive geotropism in darkness may explain the downward movement in the dark and there will be no need to relate the movements to a response to light. When the physiological state that prevails during the time that the animals show negative geotropism is changed, the downward movement will begin. The movement of *Labidocera* might be explained in a similar way. In the case of *Sagitta*, light intensity is apparently the determining factor for diurnal migration. It is to be expected that this animal will leave the surface of the sea as the light grows brighter, because it shows strong positive geotropism in bright light. It also seems clear that in the more subdued light it will begin to ascend, because it shows positive phototropism and negative geotropism in such low intensities of light. It is not clear why *Eucalanus* and *Metridia* come up near the surface in spite of the fact that they show positive geotropism in warm water in darkness.

Rose (1925) examined the reactions of

various marine planktonts to light, temperature, salinity, and chemicals. He found that *Phialidium*, *Pleurobranchia*, and *Sagitta* show no phototropism in any intensity of light, but react in a different way when there is a change in temperature and salinity. All the Crustacea of the plankton studied show a marked phototropism which is influenced by changes in temperature, acidity, and chemicals. Rose states that the diurnal migration of plankton is due to the influences of external factors. The change of phototropism with changes of light intensity and temperature is believed to be the chief cause. The effect of temperature becomes very important when it passes 20°C. As additional factors in relation to the phototropism of organisms are given salinity, chemical content of the sea water, and dissolved gases. The internal physiological condition of the animals may also be regarded as a factor.

Fox (1925) carried out experiments concerning the effects of light on the vertical movement of *Paramecium* and echinoid larvae of *Diadema setosum*. He states that these animals under certain conditions swim downward in light and move upward in darkness. Acids and alkalies have marked influence upon phototropism. Thus the phenomena already described for certain Crustacea exist not only in animals swimming by muscular movement but also in organisms moving by ciliary action. However, Kanda (1918) states that reversibility of the negative geotropism of *Paramecium* by temperature and by chemicals is extremely doubtful.

Bolin (1926) found that certain rotifers, *Mytilina spinigera* and *Rattulus rattus*, are negatively phototropic to strong as well as to weak light. Carbon dioxide has no influence upon phototropism, but the animals become positively phototropic when hydrogen sulfide is dissolved in the culture medium. It was also observed that *Mytilina*, *Rattulus*, and *Rotifer neptunius* show positive geotropism under normal conditions, while the reaction is reversed in both light and darkness when carbon dioxide or hydrogen sulfide is placed in the medium surrounding them. No chemotropism exists in these animals. Bolin states that the reactions described harmonize with the natural habits of these animals.

MIGRATION AS AN EFFECT OF PERIODIC CHANGES IN METABOLISM

In discussing the literature, it seems necessary to note another possible explanation. Menke (1911) carried out experiments with *Idothea* and found that chromatophores expand in daytime and contract at night. The periodical change of the chromatophore movement corresponding to the usual periodicity occurs even if the animals are kept in darkness. Such facts are applied by Menke to the diurnal migration of plankton. He states that the periodical migration and the periodicity of the chromatophore movements are essentially of like nature, and are conditioned by periodicity of metabolism. As has been noted, Esterly (1919) pointed out that *Acartia* exhibits a rhythmical change in geotropism that is not connected with the external conditions.

Ewald (1910, 1912) presents another point of view in regard to the causes of diurnal migration. Working with *Daphnia*, *Leptodora*, *Bythptrephes*, *Bosmina*, and the nauplii of *Balanus*, he reached the conclusion that these animals cease their locomotor movements if they come to a region where the light is too intense and therefore they sink down, and they again begin to swim upward when they reach a region of lower intensity of light. Thus the animals maintain themselves in a region of about the same degree of illumina-

tion all day long. They ascend in the evening and descend in the morning without giving phototropic reactions.

Eyden (1925) observed the daily changes in the specific gravity of *Daphnia pulex*. The maximum specific gravity was found in the morning and the minimum in the evening, Eyden states that the changes in the specific gravity may be considered as a factor in the upward and downward movement of *Daphnia*.

In concluding the review of the literature, it is proper to mention the theory of Ostwald. He (1902) states that the descent and ascent of plankton is due to the decrease and increase of the viscosity of water through its increase and decrease in temperature. Further he states that the vertical movement of plankton is not so much due to the tropisms of organisms as it is to the alternation of the viscosity of water. This theory, however, may be applied only to the diurnal vertical movements of organisms which live very near the surface and have only very limited powers of locomotion.

Still another point of view is expressed by Franz (1911, 1912, 1913). He holds that vertical movement does not occur and that animals are really as abundant at the surface during the day as during the night, but that they escape the net when it is light enough for them to see. There is not space to go more fully into this view. Many field observations show apparent diurnal migration of many species of animals in the ocean and in lakes, with the exception of very shallow and turbid ponds, or high mountain lakes.

LIGHT AND TEMPERATURE AT DIFFERENT DEPTHS IN LAKES

When the sunlight passes through the water of a lake or the ocean, it is absorbed until at some depths there is absolute darkness. The intensities of light at different depths of the sea have been measured by various observers. Recently Pool and Atkins (1926–1929) carried out measurements of the submarine illumination in the Plymouth area by means of photo-electric cells. They show that the mean value of the percentages of light in air reaching 5, 10, 15, 20, 40 and 60 meters are 37.3, 23.6, 14.4, 6.62, 0.72 and 0.085 respectively. During the observations a Secchi disc was just visible at depths of 9 to 14 meters. It has also been shown that the visibility of the Secchi disc is independent of the illumination in air within rather wide limits and that the illumination at the depth at which the disc is just visible is around 16 per cent of that in air.

In a lake in the temperate zone the surface temperature rises steadily from the end of March until August, when it reaches a maximum. At this period the temperature of the surface water is generally around 20°C., while at depths of 5 to 15 meters the temperature suddenly falls. This layer of sudden change in temperature is known as the thermocline or mesolimnion. Below this layer or in the hypolimnion the temperature of the water is generally lower than 10°C. In deep lakes the temperature of the bottom water is 4°C. The differences in the intensity of the light as well as in the temperature of the water at different depths must have marked influence upon the vertical movements of plankton.

For making catches of plankton it is most desirable to use the pump method. Water may be pumped up through a hose from various depths and at intervals throughout the day. The water is strained through a plankton net and all the planktonts in each catch are counted. Fifty liters of water are sufficient for this purpose. The changes in the vertical distribution of the plankton at different pe-

riods may thus be studied. But if the water is too transparent and the planktonts are found abundantly in a stratum deeper than forty or fifty meters, as in the case of the open ocean, the pump method can not be employed. In this case the vertical and horizontal closing net may be used.

IS DIURNAL MIGRATION DUE TO CHANGES IN LIGHT?

If the diurnal migration of planktonts is due largely to light, as certain earlier investigators maintained, there should be a direct relation between the transparency of the water and the depths to which the planktonts descend in the daytime, and there should also be a close relation between changes in the intensity of the sunlight and the vertical movement of plankton, i.e., the upward movement should take place at dusk and at dawn or there should be differences in the vertical distribution on rainy, cloudy, and sunny days.

Table 1 shows that such relations obtained in some Japanese lakes. In Aoki Lake, where the water was the clearest of any observed, *Diaphanosoma brachyurum* was distributed in a stratum ranging from 8 to 12 meters, while in Suigetu Lake, where the water was the most turbid, it predominated from the surface to a depth of 3 meters. The observations made on Kizaki Lake and Lake Biwa show that the more transparent the water is, the deeper the planktonts are found in the daytime. The vertical distributions of other species in Aoki Lake and Kizaki Lake are illustrated in Figures 1 and 2. All plankton crustaceans, such as *Holopedium*, *Polyphemus*, *Bosminopsis*, *Daphnia*, *Bosmina*, and *Diaptomus* are found in deeper strata in Aoki Lake than in Kizaki Lake. A similar relation has been noted by Burckhardt (1900) for *Daphnia* in Vierwaldstättersee, but Juday (1903) could not find such a relation for any migrating Crustacea in the Wisconsin lakes.

TABLE 1

The vertical distribution of Diaphanosoma brachyurum (The number of individuals in each liter is indicated)

	SUIGETU LAKE	KIZAKI LAKE	KIZAKI LAKE	LAKE BIWA	LAKE BIWA	AOKI LAKE	AOKI LAKE
Dates	16/IX/26	26/VII/27	12/VIII/25	1/IX/27	10/VII/27	16/VIII/25	20/VIII/27
Time	1–2 p.m.	2–3 p.m.	1–2 p.m.	2–3 p.m.	12–1 p.m.	2–3 p.m.	2–3 p.m.
Weather	Fine	Fine	Fine	Fine	Fine	Fine	Fine
Thermocline	5–10m.	5–12m.	5–12m.	12–20m.	12–20m.	5–12m.	5–12m.
Transparency	1 m.	4.5 m.	6 m.	8 m.	12 m.	10 m.	12 m.
0.	8.6	0	0	0	0	0	0
2	10.9	12.6	1.0	1.2	0	0	0
3	12.4	...	...	...	...	...	....
5	2.1	6.9	19.0	10.8	0.3	0.4	0
8	0.1	0.7	...	9.2	...	...	4.5
10	0	0	0	7.6	1.2	16.0	15.4
12	0	0	...	1.3	...	...	16.4
15	0	0	0	1.2	1.1	0	0
20	...	0	0	0.4	0.4	0	0
25	...	0	0	0.1	0	0	0

Some Crustacea are found nearer the surface on cloudy or rainy than on clear days. Birge (1897) made a set of observations on Lake Mendota on a day when there was an alternation of cloud and sun. During the sunny periods, *Daphnia* was found at a depth of one meter and during

the cloudy periods one-half meter. Burckhardt (1900) and Juday (1903) found a similar relation for *Daphnia* and *Diaptomus*. In Kizaki Lake *Bosminopsis*, *Polyphemus*, and nauplii were absent or very few at the surface on clear days but were found there on rainy days in as great abundance as in the evening. Russel dull days this copepod came nearer the surface.

VERTICAL DISTRIBUTION OF PLANKTON THROUGH THE DAY

Blanc (1898), Fordyce (1900), and Fuhrmann (1900) stated that in their investigations Crustacea reached a maximum of

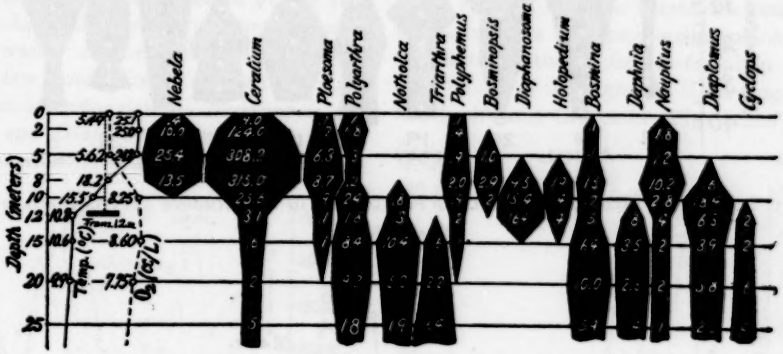

FIG. 1. THE VERTICAL DISTRIBUTION OF PLANKTON IN AOKI LAKE ON AUGUST 20, 1927

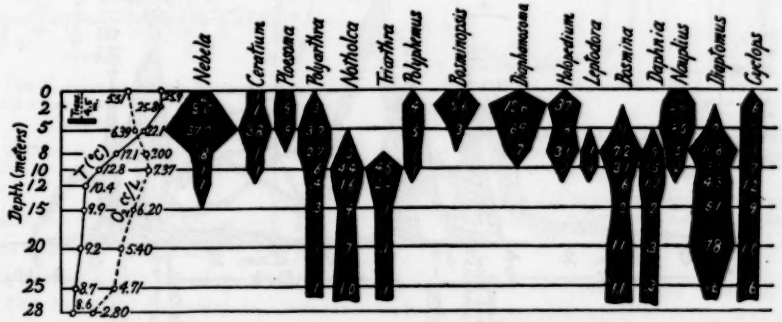

FIG. 2. THE VERTICAL DISTRIBUTION OF PLANKTON IN KIZAKI LAKE ON JULY 28, 1927
(The number of individuals per liter is indicated)

(1926) pointed out that seasonal variations in light intensity as well as the changes due to the weather have important influences upon the vertical distribution of marine plankton. Figure 3 shows that *Calanus finmarchicus* was distributed nearer the surface in April than in June and July on clear days. It can also be seen that on abundance at the surface shortly before dawn. However, later observations showed that Crustacea are found in greatest numbers at the surface at midnight or in the early hours rather than toward dawn. Ruttner (1905) first pointed out that *Hyalodaphnia Kahlbergensis* reaches a maximum of abundance at the surface twice

during the day, at dawn and at dusk. He called the type of migration with one maximum at night "nocturnal migration" and that with two maxima at dawn and at dusk "twilight migration."

tion changes. During the day the sun shone brightly. In evening the light gradually faded until the sun sank below the mountains at 5.30 p.m. The sun set at 6.30 p.m. After sunset the light suddenly

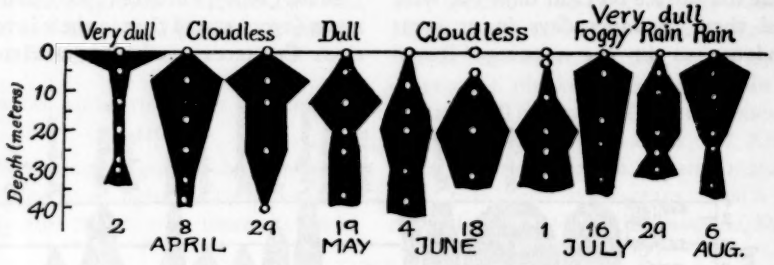

FIG. 3. THE VERTICAL DISTRIBUTION OF CALANUS FINMARCHICUS IN THE PLYMOUTH AREA ON DIFFERENT DAYS (AFTER RUSSEL)

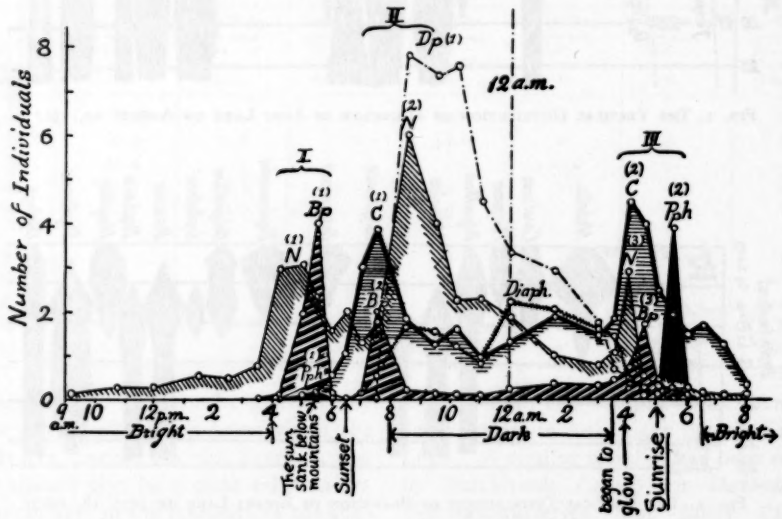

FIG. 4. THE VARIATION OF THE NUMBER OF INDIVIDUALS AT THE SURFACE OF KIZAKI LAKE ON AUGUST 6–7, 1929 (The number of individuals per liter is indicated). *N.* = *Nauplius*, *Bp.* = *Bosminopsis*, *Pph.* = *Polyphemus*, *Diaph.* = *Diaphanosoma*, *C.* = *Cyclops*, *Dp.* = *Diaptomus*

Figure 4 shows the variation in the number of individuals at the surface of Kizaki Lake at hourly or at half-hourly intervals throughout a day and a night. Before examining the curves it is necessary to bear in mind the times at which the illumina-

began to decrease and from 8 p.m. to 3.30 a.m. it was dark and there was no moon. At 4 a.m. the eastern sky began to glow and at 5.00 a.m. the sun rose. At 5.30 a.m. the sun threw the first beam upon the lake. From these descriptions it is clear that

there were three periods of changing intensity of sunlight; in the evening, after sunset, and at dawn. In examining the curves it is apparent that the upward movement of the plankton takes place when the light intensity changes. At the first period of change in illumination, or a few hours before sunset, nauplii, *Bosminopsis* and *Polyphemus* appeared at the surface. Later there was a tendency to swim downward. At the second period, or during a few hours after sunset, the maxima of abundance for nauplii, *Bosminopsis*, *Cyclops*, and *Diaptomus* were found. After 10 p.m. the number of the Crustacea in

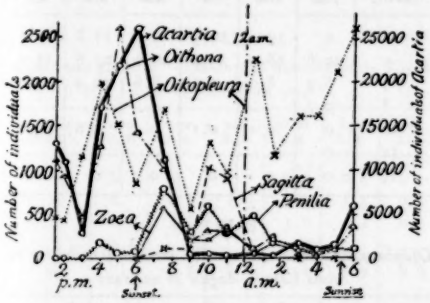

FIG. 5. THE VARIATION OF THE NUMBER OF INDIVIDUALS AT THE SURFACE OF HIRUGA LAKE ON SEPTEMBER 18–19, 1926

(The number of individuals per cubic meter is indicated.)

the plankton suddenly decreased, and at 3.30 a.m., shortly before dawn, the fewest were found. At the third period, or at dawn, the nauplii, *Bosminopsis*, *Polyphemus* and *Cyclops* came up to the surface. Nauplii and *Bosminopsis* had three maxima, and *Cyclops* and *Polyphemus* had two. These animals belong to the class of twilight migrators and seem to afford good evidence that their daily vertical movements are due largely to changes in light intensity. *Diaptomus* and *Diaphanosoma* had only one maximum. They afford examples of nocturnal migration. The frequency of appearance at the surface seems to be closely related to the depth at which planktonts are distributed in the daytime. Animals distributed in the surface layer during the day have three maxima and those found in the deeper layers have two or one. The relations will be seen in Figure 1.

Esterly (1912) and Russel (1925, 1926, 1928) showed that the maximum number of individuals of the marine plankton Crustacea at the surface is found in the early hours of the night, as is the case for the freshwater Crustacea (Fig. 5 and 6).

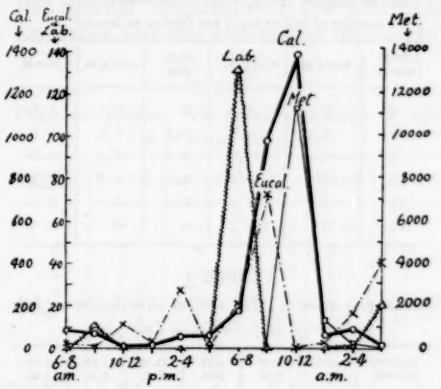

FIG. 6. THE VARIATION OF THE NUMBER OF INDIVIDUALS AT THE SURFACE OF THE SAN DIEGO REGION ACCORDING TO TIME OF DAY

(The number of individuals per hour is indicated.)
Cal. = *Calanus*, *Eucal.* = *Eucalanus*, *Lab.* = *Labidocera*. *Met.* = *Metridia*.

It is worthy of notice that *Acartia*, in which the physiological rhythm was observed by Esterly, came up to the surface a few hours before sunset and most individuals left the surface one hour after sunset. *Calanus*, *Metridia*, *Eucalanus*, *Penilia*, *Evadna*, *Sagitta*, and other marine planktonts tend to move downward at later hours.

TYPES OF DIURNAL MIGRATION

If the variation in the vertical distribution of plankton according to the time of

day is kept in mind the whole problem of migration will be clearer. There are various types of diurnal migration. Some species actually congregate at the surface at night and leave the lower water, while others merely move up into the surface layer at night; in these there is no change in the distribution of the lower water, so that they become evenly distributed from the surface downward. In some animals the distribution in daylight is somewhat modified at night but only a few individuals move up to the surface layer. There are still other types of migration. Some forms show a tendency to move upward at night but do not reach the surface layer, and others show no change in their vertical distribution throughout the day and night.

In Wisconsin Marsh (1900) observed the most marked change in the vertical distribution of the Crustacea within one half meter of the surface, while below three meters the movement was very slight. The same was observed by Ziegelmeyer (1927) in the Tegersee. Juday (1903) made observations on ten of the lakes of Wisconsin. In three of them the migrations were confined within these narrow limits, but in the other seven lakes, the change in the vertical distribution extended to deeper strata. Further he states that the movement of any species rarely affected the vertical distribution more than three or four meters below the upper limit in the daytime. Burckhardt (1900) observed the definite migration of Crustacea to the surface in Vierwaldstättersee. He showed that the plurimum of *Daphnia hyalina* was found in 20 to 60 meters in the daytime but at night was between 0 and 10 meters. *Leptodora* had a range 10 to 40

TABLE 2

Polyphemus pediculus. The vertical distribution in Kizaki Lake on August 12–13, 1925. (In tables 2–14, the number of individuals per liter is indicated)

DEPTH (*meters*)	2.00 P.M.	6.30 P.M.	10.00 P.M.	2.00 A.M.	5.30 A.M.
0	0.1	4.0	0	0.1	2.6
2	2.0	1.6	0.2	0.2	0.6
5	0.4	0.6	1.2	1.4	1.0
10	0	0.1	2.0	1.8	0.3
15	0	0	0.1	0	0
20	0	0	0	0	0

TABLE 3

Bosminopsis deitersi. The vertical distribution on July 28–29, 1927, in Kizaki Lake

DEPTH (*meters*)	2.00 P.M.	7.00 P.M.	9.45 P.M.	12.30 A.M.	3.30 A.M.	5.00 A.M.
0	0.1	1.5	0.1	0.2	0.4	0.7
2	5.6	1.8	0.1	0.3	1.0	5.5
5	0.3	0.5	0.2	2.1	0.5	0.4
8	0	...	...	...	...	...
10	0	0.6	0.9	0.7	2.0	1.0
12	0	...	...	...	...	...
		0	0	0	0	0

TABLE 4

Diaphanosoma brachyurum. The vertical distribution in Kizaki Lake on July 28–29, 1927

DEPTH (*meters*)	2.00 P.M.	7.00 P.M.	9.45 P.M.	12.30 A.M.	3.30 A.M.	5.00 A.M.
0	0	19.4	22.9	19.0	11.8	0.5
2	12.6	28.0	23.0	20.0	21.6	13.0
5	6.9	8.0	9.2	8.6	10.4	18.0
8	0.7	...	...	...	...	...
10	0	0.1	0.1	0.2	0.6	0.6
12	0	...	...	...	...	...
15	0	0	0	0	0	0

TABLE 5

Diaphanosoma brachyurum. The vertical distribution in Aoki Lake on August 20–21, 1927

DEPTH (*meters*)	2.00 P.M.	7.30 P.M.	10.10 P.M.	2.00 A.M.	5.30 A.M.
0	0	6.0	18.0	7.8	0
2	0	5.5	19.0	8.3	0
5	0	20.5	17.5	22.3	0.2
8	4.5	...	...	...	...
10	15.4	12.5	0.6	6.5	10.5
12	16.4	...	...	...	...
15	0	0	0	0	0

meters during the day and 0 to 10 meters at night. Tables 2 to 7 show the changes of the vertical distribution of various plankton Crustacea at different periods of the day. Tables 2 and 3 show the twilight migration. The upward movement is clearly shown in the vertical distribution at 6.30 p.m. and 5.30 a.m. in Table 2 and at 7.00 p.m. and 5.00 a.m. in Table 3. The downward movement at night was so remarkable that the plurimum was found at a depth of five to ten meters, where only a few animals were found in the daytime.

Tables 4–7 give examples of nocturnal migrations. Tables 4 and 6 show that the amount of the movement of *Diaphanosoma* and *Diaptomus* was very slight in a layer three to five meters below the upper limit of the day distribution in Kizaki Lake. But in tables 5 and 7, the same species show more marked movements in Aoki Lake. There was a general upward movement of the whole mass of the animals. The plurimum of both species had a range of from ten to twelve meters deep during the day, while at night only a small part remained in that stratum; the great majority moved upward and were found from the surface to a depth of five meters. In general, the diurnal vertical movements seem to be more extensive in transparent than in turbid lakes.

TABLE 6

Diaptomus pacificus. The vertical distribution in Kizaki Lake on July 28–29, 1927

DEPTH (*meters*)	2.00 P.M.	7.00 P.M.	9.45 P.M.	12.30 A.M.	3.30 A.M.	5.00 A.M.
0	0	0	1.8	3.0	0.4	0
2	0	0.1	1.9	4.2	1.3	0
5	0.2	2.5	4.5	3.8	3.4	0.1
8	10.8	...	...	...	...	...
10	7.1	9.8	8.5	11.1	5.9	9.6
12	4.3	...	...	...	...	...
15	5.1	7.9	4.3	6.6	7.9	7.9
20	7.8	6.9	8.0	7.3	8.8	8.2
25	0.6	...	...	...	...	...

TABLE 7

Diaptomus pacificus. The vertical distribution in Aoki Lake on August 20–21, 1927

DEPTH (*meters*)	2.00 P.M.	7.30 P.M.	10.10 P.M.	2.00 A.M.	5.30 A.M.
0	0	0	15.8	6.0	0
2	0	0	11.8	5.3	0
5	0	0.5	6.6	7.8	0.1
8	0.6	...	...	...	...
10	20.2	17.2	8.3	7.3	23.0
12	6.3	...	...	...	...
15	3.9	6.8	5.7	6.1	7.7
20	3.8	3.4	7.4	5.7	5.3
25	2.5	...	...	...	...

Russel (1925, 1926, 1928) showed that not only the Crustacea of the plankton but certain medusae, polychaete larvae and fish larvae perform definite migrations to the surface. Esterly (1912) showed that the Copepoda were distributed in deeper strata in the San Diego region than the Plymouth area, and as a result the extent of the vertical movements was greater.

Birge (1895) and Juday (1902) state that the diurnal migration of the plankton Crustacea was not affected by moonlight in Wisconsin lakes, but Russel (1926) found that certain animals, especially fish larvae, showed a more marked movement upward on moonless than on moonlight nights.

THE EFFECT OF THE THERMOCLINE

The vertical movements of *Diaptomus*, *Cyclops*, *Diaphanosoma*, *Holopedium*, *Bosmina*, some species of *Daphnia*, *Polyphemus*, and almost all marine planktonts seem not to be affected by the thermocline or the changes in temperature of water. However the migrations of some species show noteworthy exceptions.

Juday (1903) found *Limnocalanus macrurus* distributed in the daytime below a depth of fifty meters in Green Lake. It began to move upward at night, but when it reached the thermocline, further upward movement was clearly retarded. Juday made similar observations on *Daphnia longiremis* in Okauchee Lake, *D. pulicaria* in Lake Mendota and in Winona Lake, *D. retrocurva* in Lake Mendota, and *D. hyalina* with round helmet in Rainbow Lake. Birge (1897) was also unable to find a diurnal migration of *D. pulicaria* in Lake Mendota. The effect of the thermocline upon the vertical distribution of *D. pulicaria* is more clearly shown when the seasonal changes in vertical distribution are studied (Birge, 1897; Juday, 1903). Juday noted, for instance, that the thermocline was two meters deeper in October than in August in Oconomowoc Lake and the day position of *D. pulicaria* was likewise found two meters deeper. About the middle of June it was found much nearer the surface.

In Japanese Lakes *Daphnia longispina* is generally distributed below the thermocline (Table 8). It apparently shows a tendency to move upward at night, but not a single individual was found above a depth of five meters or in the epilimnion at night (Table 9). However, *Daphnia longispina* came up near the surface in winter when the temperature of the surface water decreased (Table 8).

There are still other types of diurnal migration which seem to be affected by the thermocline. In the first type, the depth to which the animals descend in the daytime does not depend upon the intensity of the sunlight. Plankton occupy the lower part of the mesolimnion on cloudy as on

TABLE 8

The vertical distribution of Daphnia longispina, illustrating the effect of the thermocline

Lakes.....	Kizaki L.	Kizaki L.	Aoki L.	Aoki L.	L. Biwa	Noziri L.	Kizaki L.	L. Mendota
Dates.....	12/VIII/25	26/VII/27	16/VIII/25	20/VIII/27	6/X/26	20/VIII/28	5/XII/25	Aug. 1895
Thermocline ...	5–12m.	5–12m.	5–12m.	5–12m.	12–20m.	12–15m.	15–20m.	(Birge)
0	0	0	0	0	0	0	0.1	0
2	0	0	0	0	0	0	0.3	0
5	0	0	0	0	0	0	0.5	
8	...	0.9	...	0	0	0	...	11.0
10	10.4	1.5	1.2	0	0	0	0.5	
								65.0
12	...	1.2	...	0.8	...	0	...	22.0
15	7.0	0.2	1.8	3.5	0	0.1	0.5	
								1.6
20	0.1	0.3	0.8	2.6	0	0.1	0.2	
25	0.1	0.3	0.5	1.4	0.2	...	0.1	
30	0.1	...	0.2	...	0.8	...	0	
	(28m.)	(28m.)					(28m.)	

TABLE 9

The vertical distribution of Daphnia longispina in Aoki Lake on August 20–21, 1927

DEPTH (*meters*)	TEMPERATURE	2.00 P.M.	7.30 P.M.	10.10 P.M.	2.00 A.M.	5.30 A.M.
0	25.1	0	0	0	0	0
5	24.8	0	0	0	0	0
8	18.2	0	...	...	...	...
10	15.5	0	0.2	6.5	4.2	0.8
12	10.8	0.8	...	...	...	...
15	10.6	3.5	5.5	4.5	6.0	9.0
20	9.9	2.6	2.3	4.0	3.8	6.8
25	9.1	1.4	...	...	...	...

sunny days. However, during the upward movement at night there is no evidence of influence of the thermocline. For example, *Epischura* and *Leptodora* in Winona Lake and *Mysis relicta* in Green Lake and Trout Lake are found in the lower part of the thermocline and do not change the day position on cloudy as on clear days, while they were found in surface catches at night (Juday, 1902, 1927). In another case, the thermocline apparently prevents the downward movement of the animals in the daytime. Birge (1897) states that in Pine Lake and Oconomowoc Lake, in both of which many Crustacea range through the thermocline, *Diaphanosoma* is confined to the region above it. March (1897) found that *Epischura* had a similar distribution in Green Lake.

DIURNAL MIGRATION IN WINTER

As the thermocline has a marked influence upon the vertical movements of planktonts, it would be expected that the diurnal movement in winter would differ from that in summer. The planktonts are distributed evenly in winter from the surface downward and the upper limit of the distribution is found very much nearer the surface, owing to the weakness of the intensity of the sunlight and to the circulation of the water by strong winds. As a result diurnal vertical movements are found only in exceptional cases.

In Kizaki Lake, with the exception of an apparent migration of adult *Diaptomus*, it was impossible to detect any vertical movement of the plankton Crustacea on December 5 (Table 10).

When the lake is covered by ice, the water again becomes stagnant. During this period zonal vertical distribution is found as in the case of the summer period of stagnation. But when the ice is covered with snow the lake becomes dark even at the surface layer. Then the animals are distributed evenly from the surface downward. Ruttner (1909) showed that *Diaptomus* was more uniformly distributed in the Grösser Plöner See when the ice was covered with snow (Table 11). Behrens (1914) found an apparent diurnal migration of the Copepoda under the ice covering in Sakrower See. The maximum of abundance at the surface was found at midnight (Table 12).

TABLE 10

The vertical distribution of adult Diaptomus pacificus in Kizaki Lake on December 5, 1925

DEPTH (*meters*)	TEMPERATURE	12 M.	4 P.M.	10 P.M.
0	8.2	0.4	0.1	2.0
2	8.3	0.9	1.2	1.8
5	8.2	1.3	1.1	2.0
10	8.2	0.4	1.1	0.7
15	8.1	0.9	1.3	0.6
20	6.7	0.7	1.5	0.4
25	5.6	0.4	0.5	0.2
28	5.6	0	0.1	0

TABLE 11

The vertical distribution of Diaptomus in Grösser Plöner See, illustrating the vertical distribution under the ice covering with and without snow (After Ruttner)

DEPTH (*meters*)	JAN. 20, 1909 ICE.....20CM. SNOW..... OCM.	FEB. 13, 1907 ICE..... 25 CM. SNOW..... 9 CM.
0	0.3	4.4
2	11.0	4.1
5	11.0	4.3
10	1.6	3.6
20	0.6	2.5
30	4.5	5.4

DIFFERENCES IN DIURNAL MIGRATION BETWEEN ADULTS AND YOUNG

The difference in the vertical distribution and the diurnal migration between adult and young Crustacea has been observed by various workers. Birge (1897) found in Lake Mendota that young *Daph-*

nia predominate in the higher levels over the adults. Burckhardt (1900) and Juday (1903) made similar observations on *Daphnia* and Kikuchi (1927) on *Diaptomus* and found further that the young usually reach the surface earlier in the evening and remain there later in the morning than the adults. Table 13 shows the vertical distribution of young and adult *Diaptomus* in Kizaki Lake in the daytime. Table 14 shows the time at which the young and adults reach the surface in the evening and leave there in the morning in Kizaki Lake.

TABLE 12

Vertical distribution of copepods in Sakrower See on February 23–24, 1912. (After Behrens)

DEPTH (*meters*)	1.30–3 P.M.	5–6	7–8	10.30–11.30	1 A.M.–2.30	4–5	6–6.30	7–8	8–8.30	1–2 P.M.
0	0	2.1	28.1	95.0	138.0	36.0	25.3	12.6	1.3	0.1
1	5.2	1.8	5.6	45.0	81.0	33.0	33.2	8.6	1.9	0.1
3	...	4.8	6.4	26.7	60.0	16.6	11.8	10.8	3.6	1.9
5	7.3	4.2	9.2	17.1	27.2	14.2	15.2	16.7	8.3	1.6
10	2.5	3.0	15.4	8.8	5.4	7.6	...	15.0	6.0	3.2
15	4.2	6.6	10.3	2.6	5.1	5.8	...	9.6	...	4.2
20	8.6	8.5	8.7	5.2	3.8	4.6	...	10.0	...	4.0
25	10.8	19.3	8.2	5.7	2.9	3.9	...	5.2	...	3.6
30	19.1	17.4	9.7	4.4	4.9	3.0	...	5.1	...	7.2
33	61.0	73.0	89.0	34.0	78.0	17.0	...	9.0	...	16.0
35	...	...	...	...	...	...	...	...	...	60.0

TABLE 13

Vertical distribution of Diaptomus pacificus in Kizaki Lake at 2 p.m. on August 12, 1925

Naup. = Nauplius, Y.1. = Young, 0.4–0.5 mm. long, Y.2. = Young, 0.55–0.65 mm. long, Y.f. = Young female, 0.75–0.9 mm. long, A.f. = Adult female, 1.2 mm. long, Y.m. = Young male, 0.8–0.85 mm. long, A.m. = Adult male, 1 mm. long

DEPTH	NAUP.	Y. 1.	Y. 2.	Y. F.	Y. M.	A. F.	A. M.
0	0.1	0	0	0	0	0	0
2	0.5	0.1	0	0	0	0.1	0
5	4.0	0.1	0	0	0	0.1	0.1
10	2.4	4.4	3.6	1.6	0.3	1.6	2.8
15	0.3	0.6	2.8	2.0	0	2.8	0.2
20	0	0	0	0.4	0	0.3	0
25	0	0	0	0.1	0	0	0
28	0	0	0	0	0	0	0

On the basis of laboratory experiments Dice (1914) pointed out that the young of *Daphnia* showed more strongly marked positive phototropism and negative geotropism than the adults. Rose (1925) also observed that the young *Daphnia* exhibited a decided positive phototropism while the oviparous females showed negative phototropism. These reactions may probably tend to cause the young to be found nearer the surface than the adults. On the other hand, Southern and Gardiner

TABLE 14

The change of the number of individuals of Diaptomus pacificus at the surface layer in Kizaki Lake on August 6–7, 1929

	6.30 P.M.	7.00	7.30	8.30	9.30	....	1.30 A.M.	3.00	3.30	4.00	4.30	5.00
Naup.	2.0	1.3	1.7	6.0	4.1	....	1.0	0.8	1.1	2.9	0.5	0.3
Young	0	0	0.2	3.7	6.3	....	2.1	1.5	0.5	0.3	0.1	0
Female	0	0	0	2.4	0.7	....	0.4	0.2	0.1	0	0	0
Male	0	0	0	1.6	0.4	....	0.4	0.1	0.1	0	0	0

(1926) found in Lough Derg that the adults of *Daphnia hyalina* were distributed in a higher level by day than the young and that the latter made a greater vertical movement than the adults. In Kizaki Lake the nauplii of *Cyclops* were found near the bottom, while the adults were distributed in the upper strata.

Russel (1928) states that the vertical distribution appears to differ for the two sexes of *Calanus finmarchicus*, the males tending to avoid the surface layer more than the females. The freshwater Copepoda seem to show no marked difference in the vertical distribution of the two sexes.

IRREGULARITIES IN DIURNAL MIGRATION

The type of diurnal migration shown by each species is fairly uniform from day to day in each lake, though the actual depth may vary, owing to changes in the intensity of the sunlight or in the transparency of the water. In some species, however, irregularities have been observed. Juday (1903) states that *Daphnia hyalina* with round helmets showed no diurnal migration in Rainbow Lake, that those with pointed helmets did, while the reverse of this was true in Okauchee Lake, and there was a movement of both varieties in Nagawicka Lake. *Daphnia pulicaria* remained in cold water in Lake Mendota and showed no vertical movement, but in Oconomowoc Lake and in Okauchee Lake the same species apparently made a diurnal migration extending through twelve meters.

The writer found that *Holopedium gibberum* showed an apparent movement in the summer of 1925 and 1927 in Kizaki Lake, but no movement was observed in 1929 in the same lake nor in Aoki Lake in 1927. *Cyclops strenuus* was distributed below the thermocline and showed no movement in Kizaki Lake in 1925, but in 1927 in the same lake and in Aoki Lake it was distributed evenly from a depth of two meters downward and showed a diurnal migration. Whether the causes of the irregularities in the vertical distribution and diurnal movement are to be found in internal or external factors is not certain. But the facts presented show that the diurnal migration is changeable in the lakes.

The diurnal migration of diatoms, flagellates, Protozoa, Rotatoria, and other organisms which have very weak locomotor activity has been observed, but the extent of the movement is confined within narrow limits. *Ceratium* and *Anuraea* make somewhat extensive movements.

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PHENOLOGY AND ONE OF ITS MODERN DESCENDANTS

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Contribution from the Zoological Laboratories, University of Illinois, No. 370

FOR savage and uncivilized man the flowering of certain plants and appearance of certain animals must have been an important guide to hunting, fishing, fruit gathering and primitive agriculture. The time of flowering and fruiting of various plants is still an important guide to many agricultural operations. Part of the work of several important weather stations still consists in recording the status of certain flowering plants, grown for the purpose of adding biological data to that obtained from instruments.

Calendars of periodic events have been used in connection with agricultural practice for thousands of years. Becquerel (1853) describes several calendars. A Chinese calendar of 700 B.C. does not differ essentially from some spray calendars of twenty-five years ago. According to this Chinese calendar, swallows arrive in the Hoang Ho Valley from the 9th of April to the 8th of May. According to a Roman calendar of 45 A.D. they arrive in Spain the 21st to 28th of February. The Chinese and Roman calendars were compared with a Moorish calendar for Spain of 961 A.D. which recites the agricultural operations and periodic events of each month. Becquerel also discusses a calendar for Spain of 1551 and was able to draw some general conclusions from these several in accord with his own observations and those of other European workers. In the first half of the nineteenth century attention appears to have centered upon a generalization as to the relations of a given periodic event, as for example the flowering of a particular widely distributed plant, or appearance of a particular animal to altitude and latitude. Thus in 1830 according to Hopkins (1918) Schubler found that between Parma, Italy, and Greifswald, Prussia, periodic events were later in spring by four days for each degree of latitude and for each 100 meters of altitude. Hopkins finds also that Fritsch stated a similar principle in 1866. Hopkins' own work is applied to the prediction of the dates free from infesting stages of the Hessian fly. His work is, however, directly descended from the earliest type of observation, carried on without thermometers or other instrumental studies.

RÉAUMUR AND THE SUMS OF TEMPERATURES

The line of particular investigation with which we are concerned represents a series of ideas which grew out of the use of the thermometer and other instruments in connection with observations of periodic events in plant and animal communities. It is, therefore, an offshoot from the series of researches which we have discussed above. The rain gage was early used, but effective work with temperature awaited Galileo's invention of the hermetically sealed alcohol instrument about 1612 A.D. This was commonly known as the Florentine thermometer, and one scale division represented one thousandth of the volume of the lower bulb, the zero being essen-

tially the upper limit of the bulb. The series of studies with which we are concerned evidently began with the observations of the thermometer by M. de Lahire, astronomer and famous member of the Academy of Science of Paris, who published observations of heat and cold for the year 1696 in *l'Histoire de l'Academie* for that year. At the death of M. de Lahire in 1718 the observations were continued by M. Yaraldi, his nephew. He was followed by the illustrious naturalist Réaumur, who recognized that the temperature observations of that period lacked fixed points or standards to make them comparable. He therefore used the freezing point of water, as Newton and Fahrenheit had already done, for the starting point. He marked this 0 and made each scale division represent 1/1000 of the volume of alcohol in the bulb and tube below his zero. It happened that with the quality of alcohol which he used, water boiled at 80°. In 1735 he published a considerable series of readings of the thermometer taken in the morning at about 6 o'clock and about 2 o'clock in the afternoon. On page 746 he states the sums of mean daily temperatures for April, May, and June—the months in which grain and grapes make their principal growth. He compares 1734, a year with large sums of temperature, with 1735, a year with small sums, and points out a half month's difference in the maturation of fruit and grain. He advocated the use of the sums of mean daily temperatures in comparing different climates and estimating the time of maturing of plants.

During the century following Réaumur's first publication on this subject, Becquerel states that several investigators carried on observations from the same point of view as Réaumur but differed as to method of determining the sum of mean temperatures. He refers, however, to de Candolle, who began his work a century after Réamur, as having a different point of view. The latter advocated the use of the temperature at which a plant *begins development* as the starting point from which the sum should be computed. De Candolle was probably the first to introduce experimental work into this field. He determined the minimum temperature for the germination and growth of different seeds.

OETTINGEN AND THE THRESHOLD OF GROWTH

One of the outstanding investigations of the last half of the preceding century is that of Oettingen (1879), who wrote on Dorpat woody plants. He was doubtless influenced by the German psychologists of his time who were developing the idea of the *threshold of stimulation*. The threshold is a statistical point representing the average minimum stimulus giving a perceptible response. Oettingen did not follow the ideas of Weber as represented in Weber's Law, which has usually been interpreted as a logarithmic relation between stimulus and response, but he was probably first to apply the term *threshold* to that temperature just above which development becomes barely perceptible, and to use this temperature on the assumption of a direct proportionality between temperature and rate of development above the threshold.

In other respects he followed the suggestions embodied in Réaumur's summing of temperature and in the experiments of De Candolle on wheat and other plants. The latter found that the threshold for growth is 6°C., which has formed the base used by Merriam (1894) in working out his life zones. This is also the base commonly used by meteorologists. The summing of temperature above this base has become a regular practice in the British Meteorological Service for the grain growing districts

of Great Britain. General Strachey (1887) devised mathematical formulae for deriving the sum above 43°F. or 6°C. when only maxima and minima are given. A sum of temperatures above such a minimum should be taken by one hour or by two hour periods. If 6°C. is assumed as a threshold, temperatures below this are not supposed to produce any growth or development. The ordinary early spring day will not pass 6°C. before 10 A.M. and will fall below 6°C. about 4 P,M. For ordinary purposes, when using hour units it is sufficient to subtract 6° from each hourly reading above 6° and ignore the rest; thus with the records in table 1, the sum for the seven hours is 12 hour degrees.

TABLE 1

	10 A.M. 7°C.	11 A.M. 8°C.	12 M. 8°C.	1 P.M. 10°C.	2 P.M. 8°C.	3 P.M. 7°C.	4 P.M. 6°C.
Effective degrees.	1	2	2	4	2	1	0

Sum = 12° C.

The remaining temperatures, being below 6°C., are ignored and to secure degree days it is necessary to divide 12 by 24 which gives 0.5°C. degree days.

Various Europeans have carried on careful critical studies, employing various detailed methods of determining the total accumulated temperature necessary to bring a given plant into bloom, or to ripen a crop of grain. This total, however, was found to vary for the same stage of development of the same variety of plant from season to season. It has, however, served as an important general guide. Phenology and temperature summing met with the most unreasonable denunciations of plant physiologists of the recent past and, as Oettingen (1879) has said, they merely destroyed but provided nothing better.

TABLE 2

Determination of the alpha value by the Oettingen method

TEMPERATURE	HOURS TO COMPLETE DEVELOPMENT	ALPHA 13° PRODUCT	ALPHA 11° PRODUCT	ALPHA 15° PRODUCT
°C.				
16	833.3	2499.0	4166.0	833.0
18	500.0	2500.0	3500.0	1500.0
23	250.0	2500.0	3000.0	2000.0
28	166.6	2499.0	2832.0	2165.0

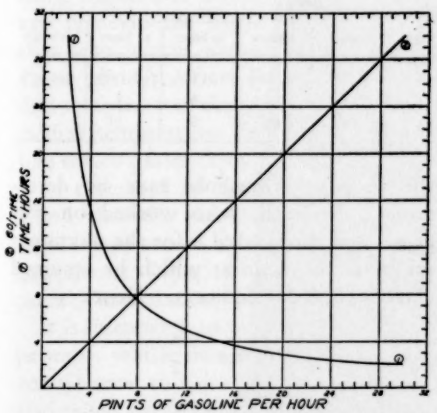

FIG. 1. SHOWING THE RELATIONS OF AN AUTOMOBILE UNIFORMLY CONSUMING ONE PINT OF GASOLINE PER MILE TRAVELING SIXTY MILES, TAKEN FROM TABLE 1

Showing the equilateral hyperbola formed by plotting time to go 60 miles and pints of gasoline on coördinates. The straight line is the reciprocal of time multiplied by sixty, the constant distance, and plotted on pints of gasoline per hour. The angle between the two axes is divided into two of 45° each. This is the relation assumed in summing temperatures. One pint of gasoline corresponds to one degree above the temperature threshold, i.e., one degree of effective temperature.

THE TIME-TEMPERATURE CURVE

The mathematical relations of the concept of sums are very simple; the assumption is that the time-temperature curve for any biological process is an equilateral hyperbola as shown in figure 1. The product of the ordinate and abscissa establishing any point is a *constant*. If an organism obeyed this law fully in its temperature

relations there would be a true *thermal constant* often erroneously mentioned in this connection. This would be the time multiplied by degrees above the threshold temperature. That the simple mathematical relations, belonging to a temperature response which Oettingen assumed, were understood is indicated by his method of determining the threshold. He merely assumed thresholds (α values) (See Table 2.) and found the products of time and temperature above them. The one which gave the most nearly constant product for all localities and years was regarded as most nearly correct. When the threshold is too low the products decrease as the temperature is higher and when the threshold is too high they increase. Thirteen degrees is the correct value in table 2.

Relative velocity is always expressed by the reciprocal of the time to do a definite amount of work or travel a definite distance. If we assume that an automobile which uniformly uses one pint of gasoline per mile goes 60 miles at various rates of speed, and let gasoline consumed take the place of temperature we have a complete parallel to the assumptions of temperature summing.

The product of time and gasoline gives a constant, the total distance, namely 60, and if the two are plotted as in figure 1 they given an equilateral hyperbola. If the reciprocals are plotted on gasoline used they fall in a straight line (See line 2 in fig. 1.) Rate of travel, which is directly proportional to the reciprocals, may be substituted for them. In this case it is, for example, 60 times the reciprocals or miles per hour.

In the case of development, temperature above the threshold has been used in the place of gasoline and is assumed to be directly proportional to the rate of development. Reibisch (1902) was one early investigator to take advantage of this in calculating supposed thresholds using the so-called straight line equation;—$XY = K$, hence $\frac{K}{Y} = X$. The threshold temperature is *unknown*, but if the temperatures in degrees centigrade are *known* in a few cases, the supposed threshold may be determined. Reibisch, who worked on fish eggs, used the symbol α for the unknown point on the scale at which he assumed there was no development. Hence

$$X - \alpha = \frac{K}{Y}$$

or

$$(X - \alpha)\, Y = K.$$

Taking table 2,

$X = 18°$ and $Y = 500$ hours

$X = 23°$ and $Y = 250$ hours,

and by substitution in the formula

TABLE 3

Automobile going 60 miles at various speeds

	TIME							
	2 hours	3 hours	4 hours	5 hours	6 hours	10 hours	12 hours	30 hours
Reciprocals of time.....	0.50	0.33⅓	0.25	0.20	0.16⅔	0.10	0.08⅓	0.033⅓
Miles per hour (60 × reciprocals).	30	20	15	12	10	6	5	2
Pints of gasoline used per hour...	30	20	15	12	10	6	5	2

$$(18 - \alpha)\ 500 = K \text{ or } 9000 - 500\,\alpha = K$$

$$(23 - \alpha)\ 250 = K \text{ or } 5750 - 250\,\alpha = K$$

$$3250 - 250\,\alpha = 0$$

$$250\,\alpha = 3250$$

$$\alpha = 13$$

Reibisch believed the results calculated in this manner were correct thresholds.

THE WORK OF KROGH

It remained for Krogh (1914), the Danish physiologist, to discover that the zero of the hyperbola or the α of Reibisch is not the threshold of development. He discovered this in working on the rate of development of fish eggs; but made an especial investigation to determine the form of the velocity of development curve using the time to complete the first cleavage plane in the frog's egg. He found that development goes on at the threshold value calculated from experiments at medial temperatures though the rates at the medial temperatures fall into a straight line which passes through their calculated α or threshold of Reibisch. He further found that the rate falls off rapidly at high temperatures, a fact brought out by Lebenbauer (1914) in the Indian corn plant (Curve similar to fig. 4).

It is interesting to note that in the same paper in which Krogh made the leading contribution to this very old concept, he also called attention to the fact that Van't Hoff's rule—a rise of 10° doubles the rate of reaction—does not hold good and is useless as a comparison. He, however, used Arrhenius' (1916) formula, a later developed law of chemical reaction. It appears that the laws of chemical reactions apply to metabolic processes when digestion of food and all activity are eliminated as in insect pupae or in animals under anaesthetics, especially after a correction is made for the circulatory and respiratory movements. According to Krogh, (1916) basal metabolism is about 75 per cent —a typographical error in Shelford ('29) made this read 25 per cent instead of 75 per cent—of the usual metabolism at 20°C. uncorrected for the involuntary muscular activities. Thus it appears that normal development with activity and feeding follow the law we are describing (Fig. 4 is typical), while standard metabolism, which is basal metabolism at different temperatures, approaches the formula of Arrhenius. Thus, as usual when scientists disagree, they are talking about different things. A decrease in rate at high temperatures is, however, evident in both standard metabolism and the metabolism of normally active animals.

This decrease in rate of development at the higher temperatures was the greatest stumbling block to success with summing temperatures. This is due to the fact that in the case of most plants and animals in the regions where summing was done, any later spring or summer day has several hours in this range of retarded rate. In the course of his study of the codling moth, Glenn (1922) found that the length of the pupal period could not be reduced below a certain minimum, but if the weather became abnormally hot its length was even increased instead of decreased. This led to summing temperature with a correction for retardation. Glenn subtracted twice the hourly temperature above 29.5° from the total degrees for the day taken by hourly means. The velocity of development curve usually assumed in summing is shown in figure 2, while that used by Glenn is shown in figure 3. His assumption was that the velocity decreased at the same rate it had increased. This gave him sums of temperature for the codling moth stages which were far more nearly uniform for the different seasons than

those obtained by the usual method (Simpson, 1903).

Krogh's work showed that for the pupa of the mealworm, an essentially constant amount of CO_2 is given off per unit weight

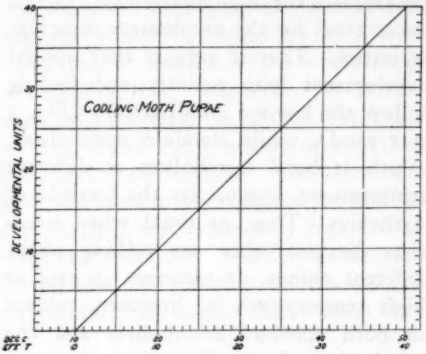

FIG. 2. SHOWING THE RELATIONS ASSUMED BY STIMPSON IN SUMMING TEMPERATURES FOR THE CODLING MOTH

A direct relation between the temperature above the threshold and the rate of development is assumed, just as a direct relation between gasoline per hour and miles per hour is assumed in figure 1. It will be noted that developmental units and degrees above the assumed threshold are of the same numerical value so that it makes no difference which is summed.

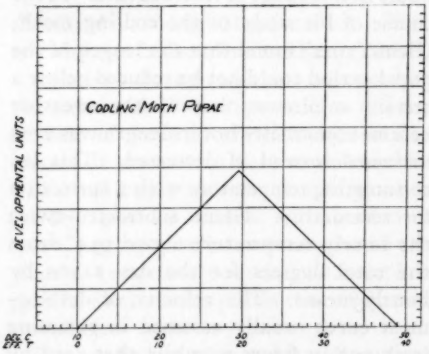

FIG. 3. SHOWING GLENN'S CURVE FOR THE DEVELOPMENT OF THE CODLING MOTH PUPA

The relations are the same as in figure 2 up to 29.5°C., but above this point developmental units and degrees are *not* of the same numerical value. It is necessary to subtract twice the amount above 29.5 to make sum of developmental units and degrees the same.

of pupae during pupal life. This laid a basis for the idea of a constant. He further stated the *straight line limits* (see 15° to 30°, fig. 4) of a series of species. This means the temperature limits for rates of development within which the century old idea of summing temperatures holds.

The discrepancy between the summing idea and the actual velocities is not confined to the higher temperatures where the rate decreases rapidly, but at the lower temperatures development goes more rapidly than would be expected. Figure 4 shows the curve for the codling moth pupa for the average humidity. Glenn (curve shown in fig. 3) compensated for the low temperature deviation from the straight line by deducting too much at the higher temperature.

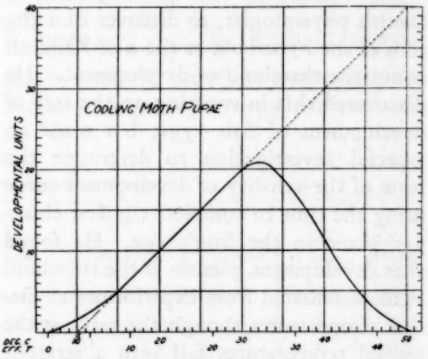

FIG. 4. SHOWING THE ACTUAL VELOCITY OF DEVELOPMENT CURVE FOR THE CODLING MOTH

Alpha is not the threshold. Between 6.5° and 16°C., developmental units and degrees above the threshold are not of the same numerical value; the same is true above 30°, which renders sums of temperatures different from sums of velocities in developmental units. This makes the summing of temperatures a very inaccurate or impossible indicator of development.

The use of inaccurate methods such as Glenn's, makes predictions uncertain in the years of exceptional conditions when pests are likely to make unusual progress.

This results in failure of remedial measures when success is most needed.

In the writer's study of the codling moth (1927), constant and variable temperature experiments were carried on so as to draw curves similar to figure 4.

[Ludwig (1928) in *Physiological Zoology* (1:358–389) states that the writer's experiments "were conducted under varying conditions found in the field and were not verified by carefully controlled experiment," whereas a large series of experiments were run over the pupal life with variation of 0.6°C. and with humidity and evaporation known and controlled. He also refers to the writer's "thermal constants," etc., where these terms are erroneous and the *Developmental Total*, was actually used.

The vertical scale of figure 4 is velocity in developmental units (see below). Between 15° and 30° C. (medial temperatures) the velocity curve is a straight line which conforms to the law of the equilateral hyperbola. Within these limits the product of time and temperature (above 10°C.) is a constant. It will be noted that the straight line portion of the curve for the codling moth pupa with its extensions is identical with figure 2, in which 10°C. is the threshold.

THE DEVELOPMENTAL UNIT

The developmental unit is the difference between the amount of development taking place in one hour at any one degree of medial temperature, and that at a temperature one degree higher, for example, between 20° and 21°C. In figure 2, developmental units and *degrees* are of the *same numerical value* so that the result is the same when one sums temperature above α (10°) or developmental units above α on the vertical scale. This is due to the fact that the reciprocal of an equilateral hyperbola divides the angle between the axes of ordinates and abscissae in half and makes an angle of 45° with each of them (see fig. 1).

To further illustrate the meaning and value of the developmental unit, the 3600 developmental units are required to complete development. This is the product of time and temperature within the straight line limits. It is completed in 360 hours at 20° (10° above α = 10°C.) and 327.27 hours at 21° (11° above α) hence one degree increase in temperature reduces the time from 360 hours to 327.27 hours or 32.727 hours.

$$\begin{array}{rl} 3600 \div 327.27 \text{ at } 11^\circ & = 11 \text{ units per hour} \\ 3600 \div 360. \quad \text{at } 10^\circ & = 10 \text{ units per hour} \\ \hline & 1^\circ = 1 \text{ unit per hour} \end{array}$$

In many cases, e.g., in the case of plants and some animals at particular periods, developmental units have a definite meaning. Thus for temperature exposures of the Indian corn seedlings (for 12 hour periods) the centigrade degree-hour-unit has a value of 0.15 mm. elongation. This is determined between 18°C. and 28°C. but above or below this range 0.15 mm. is the unit regardless of other considerations. In the case of the tree cricket (Shull) a degree (C)-hour-unit is 459 chirps. It is determined between 17° and 22°, but at high and low temperatures, the unit is merely 459 chirps.

VELOCITY CHARTS FOR TEMPERATURE AND HUMIDITY

In the case of the codling moth a large series of experiments were run at different relative humidities so that a curve for temperature effects at several different humidities, e.g., 90 per cent, 80 per cent, 70 per cent, 60 per cent, 40 per cent, etc., could be drawn. If velocity curves applicable to these humidities are cut out from cardboard and stood upright on lines labeled in relative humidity on one axis and temperature on another the surface of a (fig. 5) ridge may be formed. Height above the base is then velocity of de-

velopment. By drawing lines on the surface of the solid connecting equal heights the contours shown on figure 6 are formed, and a chart showing velocity of development at any combination of temperature and humidity is thus made by projecting these onto a flat surface. The chart is based upon constant temperatures within the sensations. Abbe, who in 1898 published an article on the curves of comfort, mentioned a chart similar in principle, which he had made but which he did not publish. Various others, especially engineers, followed with comfort charts. Pierce (1916) presented a schematic chart showing concentric ellipses corresponding to time to

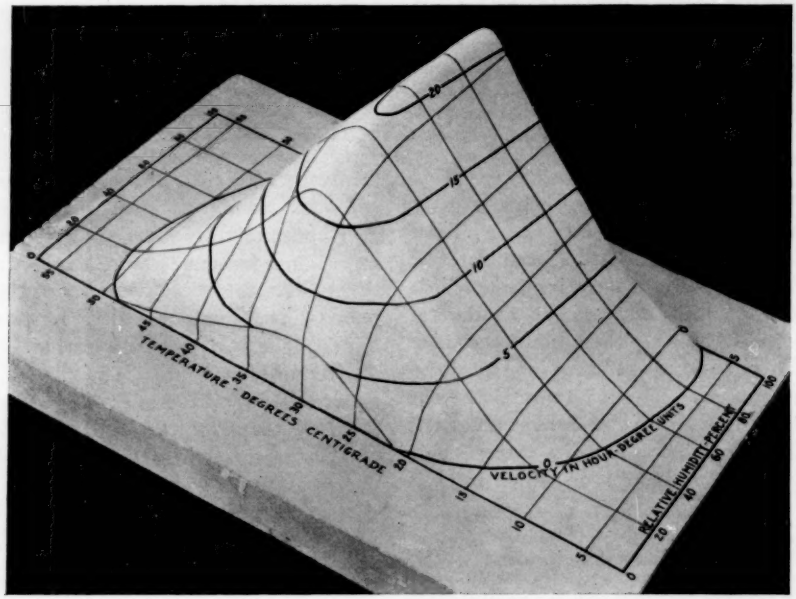

FIG. 5. SHOWING THE MODEL MADE FROM A SERIES OF VELOCITY CURVES LIKE FIG. 4, ONE FOR EACH DIFFERENT RELATIVE HUMIDITY

They were cut from paste board and fastened in position above the humidity to which they correspond and the space between them filled with plaster of Paris. The lines on the surface connect equal velocities and are contour lines running along the side and around the end of a ridge.

heavy line on figure 6, and upon variable temperatures outside of this. The central stippled areas indicate that portion of the temperature-humidity range within which the law of the equilateral hyperbola holds good.

This idea for a chart with three conditions in one plane probably originated, so far as weather and the responses of organisms is concerned, in the idea of comfort complete stages, conditions for starting hibernation, etc., on a temperature-humidity chart.

The writer applied his codling moth chart (fig. 6) to work out the dates that could have been predicted had it been used in 1915, 1916, and 1917 to predict the time of emergence at Olney, where Glenn (1922) did his work. There were hundreds of pupae whose theoretical time for

emergence could be worked out and compared with the actual time. The agreement between the two was good to a noteworthy degree (Shelford, 1927). The deviation from average rates was made clear, and it was found that rising temperatures lower development and falling temperatures accelerate it. (Shelford, 1929). Rainy autumns decrease mortality and make development more rapid the following season. Thus a new field of response is brought into recognition by establishing a standard time for the stages. Similar methods were applied in making a chart for the other stages of the life history, demonstrating that the law of summing temperatures holds for a limited range of temperature only, too small a range to permit its application to more than occasional days.

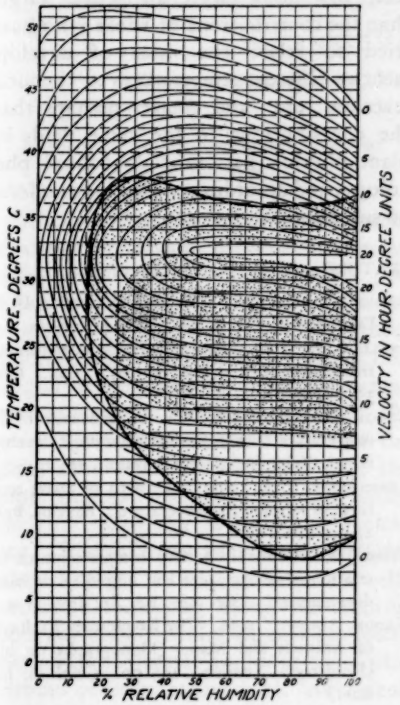

FIG. 6. SHOWING THE EQUAL VELOCITY CHART IN WHICH THE LINES ON THE MODEL IN FIG. 5 ARE PROJECTED ONTO A FLAT SURFACE

The lines connect combinations of temperature and moisture giving the same rate of development. A table was made showing the rates in developmental units by reading them off the chart for the various combinations of temperature and humidity. This was used in predicting times of appearance of moths.

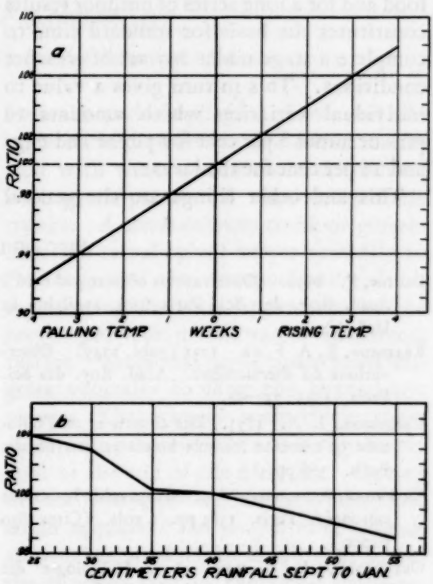

FIG. 7. SHOWING THE EFFECT OF RAINFALL (A) AND RISING AND FALLING TEMPERATURE (B) ON THE RATE OF DEVELOPMENT OF CODLING MOTH PUPAE

The evaluation of these and other factors was made possible by first evaluating temperature and moisture so that their effect was eliminated from consideration. (*a*) When temperature falls from day to day the length of the pupal life is progressively decreased; when it rises from day to day it is progressively increased. (b) Autumn and winter rainfall prepare the larvae for pupation favoring the breaking up of dormancy; perfection of this process appears to favor rapid development.

The general results show that the temperatures cannot be summed to indicate amount of development. This is best indicated in figure 4, where sum of temperature is contrasted with sum of develop-

mental units. It is not correct to refer to the sum of temperature for any process under ordinary weather conditions. This is the reason that degree-hour developmental units are necessary. The average number of these with uniform stock and food and for a long series of outdoor results constitutes the basis for standard time to complete a stage under any set of weather conditions. This in turn gives a value to individual variation which amounts to plus or minus 8 per cent for pupae and eggs and 16 per cent for the larvae.

This and other things are the general fruits of studies started with observations "*du thermomètre*" made by Réaumur almost two hundred years ago. On the whole the net result in the way of practical application to agriculture, public health, etc., has been large; altogether larger than the contributions of those who have tried to relate the rates of development at different temperatures to chemical reactions, etc., and greater perhaps than the contributions to the same fields by plant physiologists who denounced phenology, and according to Oettingen offered no substitute.

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HISTORICAL SURVEY OF THE DEVELOPMENT OF THE SYMPATHETIC NERVOUS SYSTEM (*Concluded*)

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Histogenesis of the Autonomic Nervous System (Continued)

S. Uchida ('24) studied the development of the sympathetic nervous system in birds, in mammals and in reptiles. In 48 hour chick embryos there is no trace of sympathetic primordia. The ventral roots appear as growing fibers. The spinal ganglia are developing from the neural crest as cellular strands running in the mesenchyme on the lateral aspect of the spinal cord. During the third day, the spinal ganglia have given rise to a posterior root extending as far as the ventral root. The following day shows well developed spinal nerves. A very few cells are found migrating along the ventral roots and small cellular clusters are found near the dorsolateral angles of the aorta, without communicating rami. At the end of the fourth day, there exists a continuous sympathetic chain beginning at the level of the vagal ganglion. The vagus nerve can be followed to the superior part of the oesophagus. In embryos five days old, a periaortic sympathetic net has developed but no peripheral migration is to be found. Remak's nerve originates from the aortic plexus at the base of the mesentery. Sympathetic nerve cells are found in the adrenals, in the pancreas, in the intestinal wall and in the kidneys; they are in direct continuity with the primary sympathetic chain. At the end of the same day, branches and cells of the vagus nerve form the perioesophageal plexus and the peribranchial plexus in exclusive connection with the vagus nerve and without any participation of the sympathetic trunks. A small nervous trunk originates from the sacral spinal nerves ventrally to the origin of the communicating rami, representing the first appearance of the nervus pelvicus of the sacral autonomic system. From this nerve neuroblasts migrate ventrally to form the hypogastric plexus. The primary sympathetic chain disappears progressively and is very nearly gone at the end of the fifth day. During the sixth day, the secondary sympathetic chain appears. The vagus now extends all over the stomach to the pylorus and to the superior part of the small intestine. The vagus ganglion cells are very numerous in the gastric wall, become rare at the pyloric region and are practically absent in the small intestine. The mesenteric nerves reach the intestinal tract near its ileocaecal junction. During the seventh and the eighth days the sympathetic trunks send their fibers and cells into the various thoracic plexuses, which become vago-sympathetic plexuses. The abdominal plexus is still purely sympathetic and the vagus nerves reach it only later.

This description of Uchida is very interesting and represents in fact a sort of amendment to Kuntz's theory; it considers the origin of the pulmonary, cardiac, oesophageal, gastric, hepatic and pan-

creatic plexuses as vagal; the duodenal and intestinal plexuses are purely sympathetic. He refers to an experimental investigation of his but does not give any accurate description of it. The destruction of the dorsal half of the spinal cord by the electrolytic method on one side, provokes a unilateral absence of the spinal ganglia. The sympathetic ganglia are normally formed on both sides. The prevertebral and visceral plexuses are normal as well as Remak's nerve and the vagi. We might wonder what was the result expected by the author from this unilateral destruction, about the extension and the operating stage of which he does not give any details.

In mammals, his description does not bring in very original facts. He again shows the vagal origin of the pulmonary, cardiac, oesophageal and gastric plexuses while the kidneys, adrenals, intestine, pancreas and spleen are first innervated by the sympathetic system.

C. Smith ('24) studied the origin and development of the carotid body in very complete series of mammalian embryos. The carotid bodies are innervated by a pharyngeal branch of the glossopharyngeal nerve, by the pharyngeal branch of the vagus and by numerous twigs coming from the superior cervical sympathetic ganglion. In the rat the glossopharyngeal nerve shows embryonic sympathetic cells along its course. They seem to have a really glossopharyngeal origin and do not result from sympathetic anastomoses. The vagal branch does not show any embryonic sympathetic cells until the peripheral part of the body is reached; at this point numerous sympathetic cells are given off by the sympathetic branches. In calf embryos, besides the main contribution from the cervical sympathetic ganglion, a few cellular elements of the nervous supply of the carotid body are directly derived from the ninth and tenth cranial nerves.

In an extensive paper dealing mainly with the influence of the nervous system on the limbs of the Anura, Hamburger ('28) describes a few interesting points concerning their peripheral nervous system. After having removed one half of the spinal cord in six segments at the stage of closing neural folds, he finds a complete regeneration of the dorsal quarter of the cord. The motor half is never regenerated. These results corroborate the experiments of Hooker ('17–125) and of Braus ('05). The absence of regeneration found by Harrison, Kuntz, Müller and Ingvar is probably due to the fact that in these experiments the dorsal half of the cord was removed throughout its entire length. It must be remarked that the existence of a fully round neural tube does not necessarily mean regeneration. It may be a mere shifting of the material of the uninjured half or of the nearest segments. As far as the sympathetic system is concerned, no general idea could be drawn from his results. He considers that these corroborate the theory of the origin of the sympathetic chains from the spinal cord, although in a few cases he did not find the communicating rami. It is obvious that these cases represent the result of a craniocaudal migration of the sympathetic elements from the nearest segment where a communicating ramus is found.

H. B. Adelmann ('25) studied very extensively the development of the cranial sympathetic ganglia in rat embryos. We shall consider only that of the vagus complex. This anlage is first seen in embryos of eight somites as a cellular mass interposed between the lateral edge of the neural plate and the ectoderm. At nine somites proliferation takes place and the cells migrate laterally and ventrally to come in contact with the ectoderm. Caudally the IX–X crest becomes somewhat more diffuse and is directly continuous with the spinal neural crest. Embryos of

24 somites are the first to show a definite vagal proliferation, though it is impossible to define the exact limits of it. Two cords of neural crest cells connect the glossopharyngeal and the vagal anlagen, while another strip of crest material extends caudally to join the spinal neural crest. The nodosal swelling appears at the stage of 31 somites. Some caudal extension has occurred, though, being very near the ectoderm, no direct contact can be observed between it and the vagal anlagen. The ganglion nodosum of the 34 somite embryo extends caudally over the territory of the fourth arch and bends ventrally behind the ultimobranchial body. A cellular extension of it can be traced to the root of the lung buds. The ganglion in a few sections is located close to the ectoderm without any noticeable fusion. In a 14 day embryo there is an intimate fusion between the root ganglia of the glossopharyngeal and vagus nerves. The inferior portion of the petrosal and the superior part of the nodosal ganglion are also intimately related. These connections are constant and primary, since the ninth and tenth anlagen are derived from an essentially continuous postotic proliferation of neural crest which is in direct prolongation of the spinal neural crest. There is thus no apparent contribution of any placode to the vagus ganglion; some adhesion can be found without migration of ectodermic elements.

R. A. Knouff ('27) studied very extensively the development of the cranial ganglia in the frog. His very careful and complete studies represent the most important piece of work carried out in this particular subject. We shall refer only to the development of the vagal complex. The vagal division of the neural crest grows from the dorsal border of the hindbrain downward and extends into the branchial region. When the second, third and fourth branchial pouches appear, the neural crest becomes subdivided so that each of these arches contains a small mass of cells from the non ganglionic portion of the vagal crest. This portion becomes constricted into two parts; the inferior contributes to the formation of two visceral ganglia (X and X_2). The neural crest cells of X_2 come in contact with an ectodermal thickening behind the fourth branchial pouch, which represents an epibranchial placode and probably gives a small contribution to the ganglion. The crest material X unites with two epibranchial placodes at the level of the second and third pharyngeal pouches. Above the constriction, the proximal part becomes the root connecting the vagus to the hindbrain and the distal portion differentiates into the jugularis ganglion (general cutaneous X). The dorsolateral and ventrolateral groups develop exclusively from the vagus lateral placode. The ramus intestinalis vagi is the medial projection of the visceralis X_2. Knouff concludes that the visceral innervation supplied by the vagus nerve is almost exclusively furnished by the ventral part of the vagal crest, without eliminating a possible small contribution of the epibranchial placode.

In an outstanding series of experimental researches, Stone ('22) studied the development of the cranial nerves, in order to distinguish the rôle played by the placodes and by the neural crest in their constitution. As far as the vagus is concerned, he shows that the lateral line system is derived entirely from placodic material, while the neural crest contributes to the formation of the branchial cartilages and to the general visceral portion of the vagal ganglion. This last conclusion is supported by the fact that the removal of the corresponding neural crest cells leads to a definite rarification of the visceral fibers. This experimental work of Stone is confirmed by the recent publication of Knouff.

The rôle of the placodes and the neural

crest in the formation of the cranial ganglia seems to be clearly discriminated in amphibians. In the mammalian material, however, a considerable confusion does exist, and if we take the publications of DaCosta ('23), Bartelmez ('24), Adelmann ('25) and a few others no actual theory could be drawn. The embryogenesis of the peripheral part of the autonomic nervous system has been entirely neglected in all these studies. Although the purely anatomical facts are very numerous, only a few data are known concerning the endings in the various organs and the immediate changes following the establishment of the nervous connections. In the pancreas of various mammals, the author ('25–'27) has shown that the primordia of the islets of Langerhans are very closely related to the ganglionic elements. The nervous supply of the endocrine system in the young stages of the development of the pancreas forms a well defined net, the islets being in intimate relationship with the ganglia and earning the denomination of "sympathetico-insular complexes." This pancreatic nervous network is directly continuous with the solar plexus, and the ganglionic cells are probably to be considered as true sympathetic elements. Numerous authors, for example Nelis ('26) and DeCastro ('25), tend to assume that these elements are parasympathetic in nature, and further studies are needed to discriminate the exact signification.

The rôle played by the vagus nerve in the visceral innervation has been studied very extensively from both anatomical and physiological standpoints. The anastomotic branches between the vagus and the sympathetic chain were frequently observed and analyzed. Ranson ('14), Molhant ('10), Iwama ('25), Chase ('16), Tokura ('25), Onodi ('84), Broman ('95), Edgeworth ('92), Michailow ('09), Duncan ('28), Uchida ('28) and others tried to elucidate their real nature by experimental methods. No agreement exists and further research is needed. The existence of these connecting branches does not allow any doubt, and they can perhaps explain many discordant results of physiological experimentation. The vagus nerve and the sympathetic cord might be considered as vago-sympathetic trunks, the excitation of any one of which has necessarily a complex result, making a definite discrimination of sympathetic or parasympathetic action difficult, if not entirely impossible. Besides this anatomical disposition, the visceral innervation is a difficult study on account of the variations in different groups. Bayliss and Starling ('99) have proved that the stimulation of the vagus nerve in mammals provokes a contraction of both longitudinal and circular muscles of the intestinal wall and that neither one of these contracts after excitation of the splanchnic nerves. Elliott ('04) has shown that in birds the stimulation of the splanchnic nerves is followed by a very well marked contraction of the entire duodenal region. Dixon ('02) states that in the frog the musculature of the whole stomach contracts either upon stimulation of the splanchnic nerve or after direct action of adrenalin.

It is thus impossible to generalize from the physiological results. The distinction of sympathetic and parasympathetic systems in each group requires a complete embryological and anatomical knowledge of the constitution of the nerve trunks called "vagus nerve" and "sympathetic chain." We believe the actual distinction of sympathetic, parasympathetic and local innervations to be erroneous, owing to ignorance of the real constitution of the visceral autonomic nervous system.

If we make a general survey of the literature in order to know the classical opinion

about the development of the sympathetic system, we get only a chaotic idea, even concerning the fundamental points of the question.

As far as the primary origin of the sympathetic elements is concerned, the oldest theory considered the spinal nerves as giving rise by proliferation to sympathetic cells; this viewpoint has been entirely discarded during the last twenty years and has only an historical interest.

The theory of the mesenchymal origin of the sympathetic elements was inaugurated by Remak and found only a limited number of advocates. Recently it has received a real support in the publications of Tello, who attempted to show that an important part of the sympathetic system came from a local differentiation of mesodermic elements.

Numerous observers consider the neural crest and the spinal ganglia as the exclusive source of the sympathetic cells, while others give the main rôle to the neural tube by means of migration along the motor roots. Both theories are supported by experimental studies, the results of which are diametrically opposite. These experimental researches agree in denying the mesodermal origin of the sympathetic cells. Table I summarizes these different conclusions concerning the primary origin of the sympathetic elements. It is impossible to disregard any one of the last three

TABLE 1

Primary Origin of the Sympathetic System

FROM SPINAL NERVES	SPINAL GANGLIA AND NEURAL CREST	SPINAL GANGLIA AND TUBE	MESENCHYME
Balfour, fishes	Abel, chick	Cajal, chick	Bruni, chick, rat
Marshall, chick	Allen, fishes	Carpenter and Main, pig	Camus, frog
Neumayer, *Lacerta*	Held, series of vertebrates	Froriep, *Torpedo*, rabbit	Dart and Shellshear, man
Vanwijhe, *Pristiurus*	His, man	Ganfini, series of vertebrates	Fusari, chick and mammals
	His, Jr., chick	Goormachtigh, birds	Goette, chick
	His, Jr., and Romberg, series of vertebrates	Hoffman, selachians, urodeles	Patterson, chick
	Hoven, chick	Kohn, mammals	Remak, chick
	Marcus, *Torpedo*	Kuntz, series of vertebrates	Schultze, *Vespertilio*
	Mazzarelli, birds	Rau and Johnson, sparrow	Tello, series of vertebrates
	Müller, selachians	Uchida, series of vertebrates	Weber, man
	Müller and Ingvar, chick, frog		
	Onodi, series of vertebrates		
	Rabl, *Pristiurus*		
	Schenk and Birdsall, chick, man		
	Streeter, man		

mentioned theories and any embryological investigation carried out in this field should answer the following questions:

1. Do the sympathetic chains arise from the ectoblast or from the mesenchyme?
2. Along what spinal root is there a migration of sympathetic elements?
3. Are some visceral ganglia derived from the mesenchyme?
4. What has the vagus nerve to do in the constitution of the visceral plexuses?

These four questions require a special answer for each group of vertebrates, and as far as possible need an experimental verification. The main features of the development of the autonomic nervous system will very probably be found identical in the entire vertebrate series; to them will it be possible to apply a general theory of embryogenesis and the variations found in each particular group will enable us to understand the divergent physiological results in the light of anatomical and embryological facts.

If we take into special consideration the visceral innervation, we also find a great deal of confusion, especially concerning the nervous supply of the small intestine.

TABLE 2

Primary origin of the innervation of the small intestine

MESODERM	VAGUS NERVE	SYMPATHETIC SYSTEM
Camus, frog	Abel, chick	Balfour, selachians
Dart and Shellshear, man	Kuntz, series of vertebrates	Dogiel, series of vertebrates
Fusari, chick, mammals	E. Müller, selachians, chick	Froriep, *Torpedo*, rabbit
Onodi, series of vertebrates	Stewart, rat	Ganfini, series of vertebrates
Remak, chick		Held, series of vertebrates
O. Schultze, chiroptera		W. His, man
Tello, chick, mouse		W. His, Jr., and Romberg, series of vertebrates
		Kohn, rabbit
		Meikeljohn, chick
		Neumayer, *Pristiurus*
		Rau and Johnson, sparrow
		Shenk and Birdsall, chick
		Streeter, man
		Uchida, series of vertebrates

Table 2 summarizes the main observations on this question. A mesodermal origin has been asserted by many observers, and Tello has recently given important confirmatory evidence. The primary sympathetic innervation is supported by many while the importance of the vagus nerve has been emphasized by a few noted investigators. Two other questions arise concerning this aspect of the problem:

Histogenesis of the chromaffin part of the adrenals

A complete review of the literature concerning the development of the adrenals can be found in Poll's monograph; here we shall give briefly the main conclusion of the different investigators. In this field also there has been a great deal of confu-

sion; but the actual opinion concerning the primary origin of the chromaffin elements of the adrenals seems very generally accepted.

Leydig ('53), studying the suprarenals and interrenals in fishes, concluded that the suprarenals are embryological derivatives of the sympathetic system. Remak ('57) derived the chromaffin system from the sympathetic elements. He was considering the mesodermal origin of the sympathetic system and thus the primary mesodermal origin of the chromaffin elements. Balfour ('81) in elasmobranches stated that the interrenal organs are of mesodermal origin, while the suprarenals are derived from the sympathetic ganglia located along the abdominal aorta. He was corroborated a few years later by Mitsukuri.

Gottschau ('83) in mammalian embryos noticed the intimate association of the chromaffin tissue with the cortical part of the adrenal and concluded that both are derived from the mesoderm. The same year, Janosik studying the same material observed cells of the peritoneal epithelium migrating into the mesenchyme in the region of the adrenals and stated that cortical and chromaffin components are both derived from the germinal epithelium. In mammals, Gray ('52), Valenti ('89), and Roud ('03) considered the medullary part of the adrenals to be mesodermal in origin. Minot ('94) in the human embryo found no evidence of the sympathetic origin of any part of the adrenals and supported the theory of their mesodermal origin. In reptiles von Mihalcovicz ('85) admits their common origin from the germinal epithelium. For Brauer ('00) the cortical part develops from the mesenchyme, for Weldon ('85) and Hoffmann ('00) from the pronephric epithelium, for Soulie ('03) from the peritoneal epithelium. All of them consider the chromaffin part of the adrenals as originating from anlagen of the prevertebral sympathetic plexuses. In selachians, Haller ('01) considered that the chromaffin elements of the adrenals were related to the mesonephric tubules. In the same group Semper ('75) tried to show their origin from the mesenchymal cells. Those observations were disproven by Balfour ('78) in *Scyllium* and by Hoffmann ('02), who very clearly showed the sympathetic origin of the chromaffin elements. V. Brunn ('72), Sedgwick ('80), Valenti ('93) and Minervini ('04), studying chick embryos, described the mesodermal origin of the chromaffin part of the adrenals. Schultze ('97) in *Vespertilio* described the entire adrenal anlage as originating from the sympathetic ganglia, showing only later a differentiation into cortical and medullary parts.

Fusari ('93) studied the development of the adrenals in chick and in mammals. In a 78 hour chick embryo he describes cellular bands extending from the sympathetic chains toward the region between the aorta and the cardinal veins. At 90 hours the sympathetic chains are well marked on both sides of the prevertebral region; they send numerous cellular strands toward the epithelial bands differentiated from the peritoneal epithelium. From that moment on, and still more clearly at the stage of 96 hours, the anlagen of the adrenals show their double origin, from the peritoneal epithelium and from the prevertebral sympathetic plexuses. According to Fusari, the sympathetic plexuses arise by differentiation of the mesoderm.

Soulie ('03) was unable to corroborate the descriptions of Fusari. In the 162 hour chick embryo a big ganglionic mass is located near the dorsal aspect of the interrenal anlagen at its distal end. At this moment the first distinction is to be seen between the sympathoblasts and the pheo-

chromoblasts. The topographical relations remain such to the ninth day of incubation and the penetration of the latter elements into the interrenal substance occurs only around the tenth day. Flint ('00) in pig embryos showed that the cortical develops first, the medullary appearing later as a grouping of cells wandering in from the outside. He required further proof before admitting the sympathetic origin of these migrating elements. Aichel ('00) says that in selachians the interrenals alone are homologous to the adrenals of higher vertebrates and that they arise from the peritoneal invaginations of the prenephros; the so-called suprarenals would be derived from retrograding canals of the latter organ. In mammals both parts of the adrenals are derived from the epithelium of the pronephric tubules. Wiesel ('01), though studying too far developed pig embryos, observed that the cortical part is derived from the peritoneal epithelium, the chromaffin medullary part from the prevertebral sympathetic plexuses.

H. Rabl ('91) in birds considers the chromaffin cords of the adrenals as originating from the penetration into the interrenal anlagen of the elements of a large ganglion closely related to it. This ganglion is the result of a migration of numerous indifferent cells from the prevertebral sympathetic ganglia. Soulie ('03) studied the histogenesis of the adrenals in various reptiles. In a 10 mm. long embryo of *Lacerta* the first lumbar ganglia send out a few cellular bands which become connected with one another and form a big cell-mass located dorsally to the anlagen of the interrenal system. A certain amount of connective tissue between the two anlagen establishes a clear distinction. The chromaffin part of the adrenals originates directly from the lumbar sympathetic ganglia.

Brauer ('03) described at length the development of the adrenals in *Hypogeophis*. Cellular groups become detached from the sympathetic ganglia. The cells are very clearly distinguished by their size, their granular cytoplasm and their avidity for stains. These cells migrate along the lateral and ventral aspects of the aorta, and come in intimate connection with the interrenal system.

Kohn ('03) studied very extensively the development of the chromaffin part of the adrenals in various mammals. In a human embryo, 19.5 mm. long, he describes numerous cellular groups extending from the sympathetic ganglia toward the region of the aorta. The differentiation of these elements begins in the ganglia, from which they migrate as cellular strands. At this stage, they are found only in the region of the adrenals, although a few chromaffin heaps may exist independent of the interrenal anlagen. In a 27 mm. embryo, the migration of the prechromaffin elements is found in the entire length of the sympathetic chains.

Bruni ('12) describes the first appearance of chromaffin cells in *Rana esculenta* at the stage of 27 mm. near the renal vein, in intimate contact with the lymphoid tissue of the mesonephros and the interrenal cord. He is unable to see any chromaffin heaps in the cephalic and cervical regions. Zuckerkandl ('12) presents a complete review of the literature concerning the chromaffin tissue. In a 19 mm. human embryo he verifies the description given by Kohn in a pig embryo 44 mm. in length. The chromaffin elements of the intercarotid gland are derived from cells situated in the nerves coming from the upper cervical sympathetic ganglion and forming the plexus intercaroticus. In the ganglia of the abdominal plexuses, the differentiation of chromaffin bodies begins at a time when the sympathetic cells have not yet

diverged from the original sympathochromaffin type (= sympathogeny). The statement of Soulie ('03) that the chromaffin cells do not develop until neuroblasts are present in the sympathetic ganglia can only be accepted as referring to the medulla of the adrenals, which is remarkably late in its differentiation.

Kuntz ('12) described extensively the development of the adrenals in the turtle. During the eleventh day of incubation, sympathetic cells migrate along the lateral surfaces of the aorta and may be observed in very close contact with the anlagen of the cortical substance. Later on, the prevertebral sympathetic plexuses develop and numerous cell groups may be traced from them toward the dorsal and mesial surfaces of the adrenals. A few cells are found among the cortical cells. These facts show very clearly the origin of the chromaffin part of the adrenals from sympathetic elements, which are identical with the "indifferent cells" found in the prevertebral plexuses. The chromaffinity appears only after a considerable interval of time of association with the cortical substance. It is, therefore, probable that the differentiation of those cells into chromaffin elements is stimulated by the influence of hormones produced by the cortical cells.

A. Jona ('13) studied the development of the interrenal and chromaffin tissue in the anuran amphibia. That question had been already studied by Srdinko, who described the first appearance of the interrenal system at 9 mm., by Soulie at 32 mm. and by Albrand at 29 mm. Soulie ('03) does not believe in the existence of chromaffin cells in the adrenals of the Anura in spite of the very clear observations of Giacomini ('02), Stilling ('98) and Grynfelt ('04.) At 5 mm. the interrenal organs appear as a massive proliferation at the base of the mesentery. This cellular mass increases gradually in size and progressively detaches itself from the peritoneal epithelium, lying thus at the origin of the coeliac mesentric vessels. Using the determination of partial length, i.e., from the apex of the head to the anal opening, she describes at 1 mm. isolated cells definitely different from the mesenchymal cells and showing the cytological characters of sympathogonies. It is only at 4 or 5 mm. that these cells differentiate either into phaeochromoblasts or into sympathoblasts. The chromaffin reaction is found in embryos of 3 to 12 mm. in partial length.

Hays ('14) studied the development of the adrenals in the chick. In a five day embryo, large, deeply stained cells are seen migrating ventrally from the prevertebral sympathetic plexuses, passing between the aorta and the groups of cortical cells. At 130 hours of incubation, a few of these sympathetic elements are penetrating into the cortical anlagen and become scattered throughout its substance. The first cellular differentiation is found in seven day embryos. The cells become smaller, their shape irregular, and they show a marked avidity for stains with a tendency to arrange themselves in cords. These cords break down, and during the ninth day most of the cells are found in small groups arranged around the venous blood vessels. From that moment on, no changes are found in the disposition of the two substances. The chromaffin part of the adrenals is derived from indifferent cells, which wander in from the anlagen of the prevertebral sympathetic system.

In dealing with the literature of the sympathetic system, we have already referred to the publications of Whitehead ('03), Rau and Johnson ('23), Goormaghtigh ('24) and Da Costa ('17). Their ob-

servations show conclusively that the chromaffin elements are derived from the sympathetic anlagen.

Actually it may be considered proved that the medullary part of the adrenals arises from sympathetic elements migrating toward the mesodermal primordium of the cortical substance. Table 3 summarizes the main opinions, and it will be seen that the theory of the mesodermal origin of the chromaffin part of the adrenals is no longer advocated.

TABLE 3

Origin of the Chromaffin Part of the Adrenal

MESODERMAL TISSUES	SYMPATHETIC SYSTEM
Aichel, selachians, moles	Balfour, selachians
Bruni, frog	Brauer, *Hypogeophis*
v. Brunn, chick, dog	Braun, reptiles
Camus, frog	Da Costa, chiroptera
Gottschau, mammals	De Winniwarter, mammals
Gray, chick	Fusari, chick
Haller, selachians	Goormachtigh, chick
Janosik, chick, man, cat	Hoffmann, series of vertebrates
v. Mihalcovicz, reptiles	Jona, frog
Minervini, chick, dog	Kohn, man, rabbit, cat
Rathke, crocodile	Kuntz, turtle
Roud, mouse	Leydig, fishes, reptiles
Sedgwick, chick	Minot, man
Semper, selachians	Mitsukuri, rabbit
Valenti, chick	Poll, series of vertebrates
	Remak, chick
	O. Schultze, chiroptera
	Soulie, series of vertebrates
	Srdinko, anurans
	Whitehead, pig
	Wiesel, pig, man
	Van Wijhe, selachians
	Zuckerkandl, man

A very interesting attempt has been made recently by B. H. Willier ('28) in chick embryos, to determine experimentally the origin of the chromaffin elements in the adrenals. By the method of chorio-allantoic grafts Willier shows that the adrenal formed from a four day implant is just as well differentiated as one developed from a graft taken from a nine day embryo. These results show conclusively that cells from the secondary sympathetic ganglia are not essential to the formation of the medullary cord in the chick adrenals. The sympathetic cells found at four days close to the cortical anlage represent the real primordium of the medullary system. He then questions the significance of the contribution from the secondary chain. This method of approach is a very promising one and it may give the answer to many important questions of embryogenesis of the adrenals and of the autonomic system.

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

BRIEF NOTICES

EVOLUTION

THE ASCENT OF HUMANITY. *An Essay on the Evolution of Civilization from Group Consciousness Through Individuality to Super-Consciousness.*
By Gerald Heard. *Harcourt, Brace and Co.*
$3.00 5⅝ x 8½; xiv + 332 *New York*

The author conceives the ascent of humanity to be a progress based on the evolution of psychical factors, leading from group consciousness through consciousness of the individual to a superconsciousness. He argues that in the most primitive forms of society all individuals were submerged in undifferentiated groups, societies which in many respects were analogous to communities of bees and ants. In the course of time, a consciousness of individuality emerged, at different times in different groups and under varying conditions, the earliest types being exemplified in the priest, doctor and king. In the present era, the scientific age, a higher form of consciousness is growing out of individualism, which seeks "not to acquire but to understand by a coöperative method." Just where this new form of consciousness will lead humanity is doubtful. How successful will it be in wrestling with the "consciousness of individualism," which is still bursting forth with increasing vigor?

The author's concept is well worth considering in that he gives us a comprehensive survey of the progress of humanity from quite a new angle and raises numerous interesting problems. Many will disagree with his concept of superconsciousness and will lose interest in the latter part of the book where he leads the reader into a discussion of the value of psychic research.

MODERN MATERIALISM AND EMERGENT EVOLUTION.
By William McDougall.
D. Van Nostrand Co., Inc.
$2.75 5½ x 8½; x + 249 *New York*

The author contributes this volume as a supplement to his *Body and Mind* recently noted in these columns. The contents were delivered as a series of lectures before the Louisville Presbyterian Seminary. McDougall continues to be one of the doughtiest examples of the class of humans referred to by De Morgan as paradoxers "individuals who hold views apart from the general opinion in subject matter, method or conclusion." He is an in-

trepid defender of a whole gamut of paradoxes running from Nordic Superiority to Psychical Research. In this work he espouses "teleological causation" as against the belief that "conscious thinking cannot affect the course of physical events." He rejects not only atomic materialism and its philosophic antagonist, vitalism, but what may be fairly said to lie between the position of these two, emergent evolution. What he has to say in criticism of the last has some novelty and weight. The evidence for his own contention, however, that Mind can control the future history of matter, which includes survival of personality after death, and inheritance of acquired characteristics, is as dubious as the thesis he defends.

An appendix of technical notes makes up half of the book and there is an index.

PREHISTORIC MAN IN GENESIS. *A Study in Biblical Anthropology Giving the True Reading of the First Chapters of the Bible and a Naturalistic Interpretation of the Tradition about Adam and Eve.*

By Rev. F. deP. Castells. *Rider and Co.*
5 shillings net *London*

$4\frac{3}{4}$ x $7\frac{1}{4}$; 160

The author believes he has discovered historical facts back of the story of Adam and Eve. Adam was not the first created man, the *adam* were a group of Hindu Vaisyas whom the Elohim colonized among the aborigines of Eden. Eve was procreated in the customary way; the rib is a corruption of the text. Having broken a *tabu* by eating the fruit of the sacred trees, the settlers were exiled from Eden. We imagine that the Rev. F. deP. Castells, like some other reconcilers, will fall between two stools; his interpretation is not likely to commend itself either to the orthodox or to anthropologists.

GENETICS

VARIATION AND CORRELATION IN THE APPENDAGES OF THE HONEY BEE. *Memoir 121.*

By E. F. Phillips. *Cornell University*
Free, but edition limited *Ithaca*

$6\frac{1}{4}$ x 9; 52 (paper)

Some of the conclusions which the author gives are as follows:

For the material studied, it appears that drones are considerably more variable than are working bees. The irregularity in cell size has a direct effect on variability by bringing about a lesser degree of homogeneity in the material, from which it may be concluded that the size of the cell directly affects the sizes of various parts of the body. This effect doubtless arises from the amount of food taken, although there may be some influence from pressure of the cell walls themselves, a suggestion which cannot be proved from the present material. The hooks on the hind wings are erratic in variability.

Abnormalities in venation give additional and conclusive evidence of the greater variability of the drones, which arise from unfertilized eggs.

There is a high correlation in the plane of bilateral symmetry, less in homologous and analogous parts of consecutive segments, and still less between parts of appendages lying in a dorsoventral plane.

THE GENETICS OF THE TETTIGIDAE (*Grouse Locusts.*) (*Contribution No. 105, Department of Zoology, Kansas State Agricultural College and Agricultural Experiment Station, U. S. A.*)

By Robert K. Nabours. *Martinus Nijhoff*
4.40 guilders *The Hague*

$6\frac{3}{8}$ x $9\frac{5}{8}$; 78 (paper)

In this paper are reviewed, aside from the biology and breeding habits of the Tettigidae, the author's genetic work in the family. His experiments have dealt with some of the dominant color patterns, and the normal recessives of the following species: *Paratettix texanus, Apotettix eurycephalus, Tettigidea parvipennis pennata* and

Telmatettix aztecus. The author gives many tables pertaining to these experiments and a number of plates showing color patterns. He includes a lengthy list of references and an index.

THE CHILD'S HEREDITY.
By Paul Popenoe.
The Williams and Wilkins Co.,
$2.00 5⅝ x 8½; xiii + 316 *Baltimore*

A popular handbook of human inheritance. There is a bibliography and an index.

GENERAL BIOLOGY

THE GREAT APES. *A Study of Anthropoid Life.*
By Robert M. Yerkes and Ada W. Yerkes.
Yale University Press
$10.00 *New Haven*
7 x 10¼; xix + 652

This stately and splendidly printed volume is a monument to the industry and the critical judgment of the authors. It will stand for a long time as *the* basic work of reference for anyone interested in the biology of the primates. The literature has been thoroughly combed from classical times to the present, and brought into correlation with modern experimental work in the field, of which the senior author is the acknowledged and esteemed leader. The book is divided into six parts, of which the first is historical, and the last comparative and summarizing. The other four deal successively with the gibbon, the orang-outan, the chimpanzee, and the gorilla. It is extensively illustrated, thoroughly documented (the bibliography covers 25 double column pages), and meticulously indexed. The tone throughout is a combination of rigorous critical scepticism, accompanied with enthusiastic presentation of problems urgently awaiting study. The book is a permanently valuable contribution to the literature of biology, which does honor to its authors, and to American biology.

THE SCIENCE AND PHILOSOPHY OF THE ORGANISM.
By Hans Driesch. *The Macmillan Co.*
$6.50 5½ x 8½; xii + 344 *New York*

In this second edition, the famous exponent of vitalism summarizes in a single volume, the views originally elaborated in the Gifford Lectures of 1907 and 1908. Since that time almost every work devoted to the basic principles of biology has had something critical to say of Driesch's *entelechy*, but he continues to have a provocative effect on biologic thinking. A rereading does not modify our original impression that *entelechy* is essentially a metaphysical word for scientific ignorance. The physical explanation is applied to progressively more fundamental biological phenomena, and where it seems to finally break down, *entelechy* is called in. So far as it represents simply this negative aspect of thought, vitalism does not fall within the domain of science at all, since it appears always at the moving point where science leaves off. In this respect, it is distinctly less satisfactory as a philosophy of nature than the more recently elaborated organic philosophies popularly best known as *emergent evolution*. These latter attempt to comprehend certain positive aspects of natural phenomena not adequately represented in a strictly mechanistic idealogy. In his new preface, the author promises that this edition is brought up to date, but no consideration at all is given to the numerous criticisms that have been made of his views, nor to

rival philosophic systems that have been developed to meet the problems with which he deals. There is an index.

ZELLTEILUNG UND STRAHLUNG.
By T. Reiter and D. Gabor.
Julius Springer
18 marks 8 x 11; 183 *Berlin*

This is the most extensive independent research which has been made to test the correctness of Gurwitsch's work on "mitogenetic rays." The authors confirm the existence of an action at a distance of certain living objects upon the growth region of onion root tips and assert that this action is a radiation phenomenon in the physical sense. The book contains a great mass of detailed physical and biological observations.

DIE PHILOSOPHIE DES ORGANISCHEN BEI SAMUEL BUTLER.
By Rudolf Stoff. *Phaidon Verlag*
5 marks $4\frac{1}{8}$ x $7\frac{1}{8}$; 109 *Wien*

An account for the German reader of Butler's biological writings. His views on inheritance as a form of memory and on the personal identity of parent and offspring are adequately presented, but much of the flavor of Butler's personality is necessarily lost in a résumé.

MEAT THROUGH THE MICROSCOPE. *Applications of Chemistry and the Biological Sciences to Some Problems in the Meat Packing Industry.*
By C. Robert Moulton.
University of Chicago Press
$5.00 $5\frac{3}{8}$ x $8\frac{1}{8}$; xii + 528 *Chicago*

In this book are discussed the problems of the meat packing industry and the application of chemistry, bacteriology and other biological sciences to these problems. There is much valuable information given, in non-technical language, concerning the many phases of the industry from the keeping and curing of meats, the health of the animals, etc., to the value of the numerous by-products of the industry.

ECONOMIC BIOLOGY. *A Text for Students of Agriculture and General Biology.*
By George P. Weldon.
McGraw-Hill Book Co., Inc.
$2.50 $5\frac{1}{2}$ x 8; xi + 457 *New York*

A text book of high-school grade emphasizing facts of practical and economic importance.

DIE BINNENGEWÄSSER. *Einzeldarstellungen aus der Limnologie und ihren Nachbargebieten. Band VII: Die Biologie der Moore.*
By O. Harnisch.
E. Schweizerbart'sche Verlagsbuchhandlung
16 marks (paper) *Stuttgart*
17.50 marks (bound)
$6\frac{3}{4}$ x 10; 146

DIE BINNENGEWÄSSER. *Einzeldarstellungen aus der Limnologie und ihren Nachbargebieten. Band VIII: Der Hochgebirgssee der Alpen.*
By Otto Pesta.
E. Schweizerbart'sche Verlagsbuchhandlung
17.50 marks (paper) *Stuttgart*
19 marks (bound)
$6\frac{3}{4}$ x 10; xi + 156

HUMAN BIOLOGY

GREENLAND. *Vol. II. The Past and Present Population of Greenland. By The*

Commission for the Direction of the Geological and Geographical Investigations in Greenland. *Oxford University Press*
$14.00 (U. S. A.) *New York and London*
35 shillings net (*C. A. Reitzel, Copenhagen*)
7 x 11; 415

In this second volume on Greenland, published by the Danish Commission for investigations in Greenland, there appear the following papers: The Greenlanders of the Present Day, by Kai Birket-Smith; Intellectual Culture of the Greenlanders, by G. W. Schultz-Lorentzen; Eskimo Archaeology, by Thomas Thomsen; On the Icelandic Colonization of Greenland, by Finnur Jonsson; Old Norse Farms, by Daniel Bruun; The Finds from Herjólfsnes, by P. Nörlund.

The first paper, which is by far the longest in the group, includes not only a detailed study of present day customs, habitations, furnishings and household implements, but much concerning the influence of previous immigrations on the physical characteristics and customs of the natives. It is the author's experience that individuals of mixed blood are "superior to the unmixed Eskimos by a greater susceptibility and power of adaptation as well as by greater energy and a wider outlook in economic matters." The Polar Eskimos he believes to be more cleanly than most other Greenlanders, and the Polar Eskimos are the most northerly people of the earth. But, the author points out, poverty and lack of cleanliness go hand-in-hand, in Greenland as in more civilized countries, and these northern-most people are, in a sense, well-to-do, being a small tribe with vast hunting grounds at their disposal. Matches are now widely used by all Eskimos, the old fire-making tools fast falling into disuse. Tea is the favorite beverage of the Polar Eskimos who acquired the habit through their contact with the Anglo-Saxons, while the west coast Greenlanders hold fairly firmly to their habit of coffee drinking, which they acquired from another group of peoples.

The intellectual culture of the Greenlanders has, of course, been very greatly influenced by their contact with foreigners. This influence is especially noticeable in the linguistic field. The three factors which are the main sources of the complex ideas of the Greenlanders are observation, tradition and a vivid, impressionable imagination. With hundreds of years of battling with unusual conditions as an ancestral background, the Eskimo, within his limits, is a unique individual. He can find his way where no marks are visible. He estimates time with marvelous accuracy, not only when the sun is visible, but when it is not, by the changes of the tide. His knowledge of the lives of the animals with which he is in any way concerned is complete. He is thoroughly familiar with their habits and every detail of their anatomy.

The last four papers in the volume present many interesting and important facts concerning the ancient inhabitants of Greenland. Of especial interest is the account of the discoveries at Herjólfsnes, where evidence points to a Norse settlement at about the year 1200.

LIFE AND WORK IN PREHISTORIC TIMES.
By G. Renard. *Alfred A. Knopf, Inc.*
$4.50 6 x 9¼; viii + 228 *New York*

Speculation concerning the life and work of peoples who lived thousands of centuries ago based on a few scattering remains must at best be only an approximation to the facts as they actually

existed. This book undoubtedly furnishes material for much discussion and dissension among anthropologists. The lay reader will generally accept it as an interesting and stimulating account of ancient man's activities. The writer deals with the very earliest periods of prehistory, that is, from the origins of mankind up to that period when most civilized races commenced to record ideas in writing. His method is synthetic, considering in turn "the various activities by which man has sought to satisfy his needs and show how each was carried on until the time when it enters history not without projecting into our own times not a few curious survivals."

The book contains a number of interesting illustrating reference lists, and an index. It is one of the volumes in the "History of Civilization" series, edited by C. K. Ogden.

FROM THE PHYSICAL TO THE SOCIAL SCIENCES. *Introduction to a Study of Economic and Ethical Theory.*
By Jacques Rueff (Translated by Herman Green, with an Introduction by Herman Oliphant and Abram Hewitt).
The Johns Hopkins Press
$2.00 *Baltimore*
5⅛ x 8⅜; xxxiv + 159

The burden of M. Rueff's song is that the physical and the social sciences are alike in their essential methodology. In mechanics the concepts of mass and force and the laws of motion are created by us so that we may deduce from them the observed behavior of moving bodies. Similarly in the different systems of ethics we create God, or the categorical imperative, or the hedonistic principle, in order that we may deduce from them the rightness or wrongness of particular classes of acts which we have observed empirically to be judged right or wrong by the society in which we live. Ethical or legal or economic theories have no absolute or *a priori* validity, but are of value only insofar as we can deduce from them the observed facts of ethics or law or economic activity. We advise the social scientists to read, mark, learn and inwardly digest this little book. It will certainly save them from much vain disputation and may aid them in bringing order out of the confusion of observed social phenomena.

MARRIAGE AND DIVORCE 1927. *Statistics of Marriages, Divorces, and Annulments of Marriage. Sixth Annual Report. Department of Commerce Bureau of the Census*
U. S. Government Printing Office
15 cents *Washington*
5⅞ x 9⅛; 90 (paper)

This report presents the results of the ninth Federal investigation of marriage and divorce in the United States. The first covered the twenty-year period 1867–1886, the second 1887–1906, the third, which was to continue these to 1916, because of intervening war conditions is limited to 1916. From 1916 till 1922 reports are omitted, but beginning in the latter year they have been issued annually. The main contents are categorized under the headings Marriage Statistics, Divorce Statistics, Annulment Statistics. There are tabular and graphic analyses of the secular trends of the marriage and divorce rates, and detailed tables classifying divorces by cause, party to whom granted, duration of marriage, children affected, etc. The material included is intelligently and succinctly reviewed in the summary discussions.

DANGER SPOTS IN WORLD POPULATION.
By Warren S. Thompson.
Alfred A. Knopf, Inc.
$3.50 5½ x 8; xxi + 343 *New York*

A survey of the trends in population growth of the various nations and of the resources available to each nation to support its future increments of population. Dr. Thompson concludes that the Japanese, with a rapidly increasing population and meagre natural resources, are not likely to permit the British and the Dutch to play dog-in-the-manger much longer in Borneo and New Guinea. Nor are the Italians likely to be content with a situation in which they are kept in on every side. The remedy which he suggests is a voluntary redistribution of land and resources among the peoples of the world in proportion to their needs, a remedy which, however distasteful it may be to the nations losing territory by the process, would at least be less disastrous for them than an involuntary redistribution following another World War. This, however, will not be a permanent solution of the population problem, but will merely tide over the transition period until the practice of birth control can be adopted by the various nations.

This is an important book, which will well repay reading. However, we very much doubt whether Dr. Thompson will convince the governments of Great Britain and France of the wisdom of the policy he recommends.

THE MAKERS OF CIVILIZATION IN RACE AND HISTORY. *Showing the Rise of the Aryans or Sumerians, Their Origination and Propagation of Civilization. Their Extension of it to Egypt and Crete, Personalities and Achievements of Their Kings, Historical Originals of Mythic Gods and Heroes with Dates from the Rise of Civilization about 3380 B.C. Reconstructed from Babylonian, Egyptian, Hittite, Indian and Gothic Sources.*
By L. A. Waddell. *Luzac and Co.*
28 shillings *London*
5⅞ x 9¼; lvi + 646

According to Colonel Waddell, ancient inscriptions, interpreted in the light of the Hindu *Purānas*, reveal the true origin of civilization. The Sumerians, it seems, were an Aryan race who developed the original civilization of Mesopotamia and extended it to Egypt, Crete, Indo-Persia, and Ancient Europe. Their early kings were the originals of the gods and heroes of classic antiquity as well as of the Eddas and the Arthurian cycle. The Holy Grail found its resting place, not at Montsalvat, but at Nippur in Mesopotamia. Plainly Colonel Waddell has an Aryan bee in his bonnet, and the temptation is to dismiss him as another paradoxer. However, he knows his subject more thoroughly than most paradoxers; we shall, therefore imitate the admirable circumspection of Professor Sayce, in reviewing one of Colonel Waddell's earlier works: "The book is packed with interesting facts from the latest authorities, and the illustrations are happily chosen. Indices are all that could be desired."

L'AGRO ROMANO NEL PRIMO QUINQUENNIO FASCISTA. *Relazione sull'Incremento del Bonificamento Agrario e della Colonizzazione nell'Agro Romano dal 1° Gennaio 1923 (I) al 31 Dicembre 1927 (VI).*
Tipografia Cuggiani
20 lire 7¾ x 11½; 191 *Rome*

This beautifully illustrated work shows what has been accomplished under the Fascist régime in improving agriculture in the Roman *campagna*. Tractor-driven

modern plows that break up the subsoil have replaced primitive ox-drawn plows; swamps have been drained and wells dug for irrigation. Modern cottages have replaced the thatched *capanne*, looking like a cross between a wigwam and a bee-hive, in which the peasants formerly dwelt. Schools and churches have been built, roads laid out, improved breeds of cattle and sheep introduced. Altogether this is an impressive testimony to what the Fascists have accomplished.

UNDERSTANDING WOMEN. *A Popular Study of the Question from Ancient Times to the Present Day.*
By K. A. Wieth-Knudsen (Translated from the Danish by Arthur G. Chater).
Elliot Holt
$3.00 5¼ x 8; xv + 324 *New York*

A masculine protest against the increasing ascendancy in the Western World of the female of the species. Dr. Wieth-Knudson holds that woman has been overrated, that actually she is by physical constitution man's inferior, that she should submit to the facts, and as a corollary to the male. The data that the author offers in support of his arguments are not convincing, not even to an harassed male prejudiced in his favor.

Every cubic millimeter of man's blood contains half a million more red corpuscles than a cubic millimeter of woman's blood, and woman has relatively more water (80 per cent) in her blood than man (75 per cent). This is certainly one of the many peculiarities which by facilitating a more plentiful and rapid renewal of the bodily cells confer on man a greater mental power of resistance and a more enterprising spirit.

Just where the author obtained this information he does not tell, and we do not know. Frankly, we do not believe it is true, and the same we may say for the similar statements that make up the rest of the book.

HUMAN NATURE AND HUMAN SURVIVAL. *An Essay.*
By Thiselton Mark. *The Kingsgate Press*
2s. 6d. net 5 x 7¼; ix + 86 *London*

The author promises an argument in favor of after life and the supernatural which will be drawn from nature itself. The argument seems to be this: that man has grown up as part of the universe, of which more is knowable than known, is attuned to it, and has an instinctive impulse to reach out into it beyond the confines of his mundane life. This interpenetration with the universe requires more than ordinarily experienced nature, hence the supernatural, and more than ordinary existence, hence after life. It has several weak points; one is the premise that a wish for what is absent indicates that it exists somewhere.

PERSON UND MASSE. *Untersuchungen zur Grundlegung einer Massenpsychologie.*
By George Stieler. *Felix Meiner Verlag*
11 marks (paper) *Leipzig*
13 marks (bound)
5¾ × 9¼; 239

This is a systematic and interesting attempt to bring together and discuss critically what is known of group (social) psychology, approached from a general biological standpoint. The author takes the position that a scientific group biology is possible. The book is divided into three parts, of which the first deals with basic biological and psychological considerations and definitions. The second part discusses the relation of the individual to the group. Finally the third section treats of the group as such.

HINDU CUSTOMS IN BENGAL.
By Basanta Coomar Bose.
The Book Company, Ltd.
1 rupee $4\frac{7}{8}$ x 7; 125 *Calcutta*

This account was originally written by a high caste Hindu in 1875 for the purpose of preserving records of the customs which were then prevalent among the Hindus in Bengal. Within the last fifty years, education among the upper classes has wrought many changes in the manner of living and the beliefs of the Hindus and many of the customs herein recorded are now obsolete. The author avoids, so far as possible, any discussion of religious beliefs, holding himself to an account of the customs connected with pregnancy, birth, infancy, adolescence, marriage and death.

AN INDEX TO THE ARABIC HISTORY OF GUJARAT. *Ẓafar Ul-Wálih Bi Muẓaffar Wa A'lih by Ẓ' Abdalláh Muhammad Bin 'Omar Al-Makkí, Al-Aṣafí, Ulughkháni. (Three volumes). Being a List of Persons and Places Connected with the History of the Muslims in India Down to the Beginning of the Seventeenth Century.*
By Sir E. Denison Ross.
John Murray (Published for the Government of India)
7s. 6d. (for index) *London*
$5\frac{3}{4}$ x 9; viii + 977

This is "perhaps the most extensive list that has hitherto been published of notable personages who lived during the domination of the Muslins in India from the Eleventh to the beginning of the Seventeenth Century." The list, however, is not limited to a mere enumeration of names. In the case of famous men, and frequently, in the case of less important individuals, a résumé is given of the important events in their lives. Thus much interesting information is now available which otherwise could not be had until an English translation of the history appears.

JOHNS HOPKINS. *A Silhouette.*
By Helen Hopkins Thom.
The Johns Hopkins Press
$2.75 6 x 9; xi + 125 *Baltimore*

Mrs. Thom calls her life of one of Baltimore's most distinguished citizens, a silhouette. It is indeed fortunate that a close bond of sympathy sprang up between the author, when a mere child, and her bachelor great-uncle. Else we might not have had preserved even this meager record of a man who brought into existence the Hospital and University which bear his name, and who provided so liberally (for his time) for their maintenance. Being a merchant and a banker, with no flair for putting his ideas in writing, Johns Hopkins left few manuscripts which could supply a background for a biography. Therefore we can know little of the ideas and plans of that quiet Quaker who played such a large part in the financial, charitable and educational affairs of Baltimore. Mrs. Thom does give us, however, a glimpse of some of the remarkable traits possessed by this unusual man.

OUR FOREFATHERS. *The Gothonic Nations. A Manual of the Ethnography of the Gothic, German, Dutch, Anglo-Saxon, Frisian and Scandinavian Peoples. Vol. I.*
By Gudmund Schütte. Translated by Jean Young.
Cambridge University Press
21 shillings *London*
$6\frac{1}{4}$ x $9\frac{1}{8}$; xi + 288

The original of this volume appeared in Danish in 1926. The author's chief motive in writing the book was to supply a systematic framework for the study of

Anglo-Saxon ethnology "comparable to the German text-books of Zeuss, Brewer, Much and Kaufmann." Emphasis is put on "the strict regularity of plan" rather than on the subject matter, which is used mainly to illustrate the plan. Following the introductory chapter on "The Indo-Europeans" the arrangement of the sections is as follows: names, sub-division, ethnic position, environment, old home, language, civilization and history. The author has also sought to bring about a reform in nomenclature. There are frequent citations of literature throughout the text, an excellent index and a number of illustrations, chiefly distribution maps.

There is to be a second volume issued presently which will deal with the account of the individual Gothonic tribes and will follow the same general lines as volume one.

COLOR AT HOME AND ABROAD.
By George Mallison.
The Christopher Publishing House
$3.00 5⅛ x 7⅞; 393 *Boston*

Mr. Mallison is "all het up" over the dangers of amalgamation of the whites and negroes in the United States and proposes as a prophylactic that the negroes shall be shipped back to Africa. This solution of the race problem was, if we remember rightly, tried nearly a century ago and met with no great success. When we reflect that the proportion of negroes and negro-white crosses in the population of the United States has decreased from 19.27 per cent in 1790 to 9.90 per cent in 1920, our blood refuses to boil at the thought of the future. When amalgamation comes—as it no doubt will by degrees—we see no likelihood that the national complexion will be darker than a light tan.

ADVENTURES OF AN OUTLAW. *The Memoirs of Ralph Rashleigh, a Penal Exile in Australia 1825–1844.*
With Introductory Notes by Joseph W. Krutch and The Earl of Birkenhead.
Jonathan Cape and Harrison Smith
$3.50 5⅝ x 8⅝; xxii + 349 *New York*

The book is an extraordinary human document, if true, and we are disposed to accept it as authentic, after a careful reading. The manuscript was sent to the publishers by Mr. Charles H. Bertie, the well-known librarian of Sydney, New South Wales. It is the story of an English convict transported to Australia for life as a convicted criminal, sometime in the early part of the nineteenth century. The picture of life in the Criminal Colonies which it paints is unforgettable. "Man's inhumanity to man" is notorious, and doubtless a century from now our present penological technique will seem as horrible as Australia's of 1830 does to us now, but perhaps a widespread reading of this book might help along a little. Every student of human behavior certainly should read it.

THE LIFE OF HERMANN M. BIGGS, M.D., D.SC., LL.D., *Physician and Statesman of the Public Health.*
By C.-E. A. Winslow. *Lea and Febiger*
$5.00 net *Philadelphia*
6⅛ x 8⅝; xii + 432

A biography of the American pioneer in translating the bacteriological and immunological discoveries of the '80's and '90's into a public health program. Dr. Winslow is not one of the new style of biographers; his interest is as much in Biggs' professional work as in his personality. Nevertheless, from the mass of detail presented there emerges a clear view of the man as well as an interesting narrative of what he accomplished.

MAN AND CIVILIZATION: *An Inquiry into the Bases of Contemporary Life.*
By John Storck. *Harcourt, Brace and Co.*
$3.75 5½ x 8½; v + 449 *New York*

An excellently written account of the biological, psychological, and sociological factors in civilization, intended for a college orientation course. The chapter on science contains one of the best brief treatments of scientific methodology that we know of. There are bibliographic notes at the end of each chapter and an index.

MAN AND SOCIAL ACHIEVEMENT. *An Introduction to Social Evolution.*
By Donald C. Babcock.
Longmans, Green and Co.
$3.00 5¼ x 7¾; xi + 546 *New York*

An account of how man came to be what he is in his social, economic, and other cultural activities. There is an appendix with questions for discussion, topics for investigation and readings on each chapter. There is also an index.

SOCIAL RESEARCH. *A Study in Methods of Gathering Data.*
By George A. Lundberg.
Longmans, Green and Co.
$3.00 5¼ x 7¾; xi + 380. *New York*

A discussion of the planning of schedules, the carrying out of case studies, problems of terminology, units and classification and other questions involved in the gathering of data for the social sciences. There are a bibliography, a source list of social data, and author and subject indexes.

PAPAGO MUSIC. *Smithsonian Institution, Bureau of American Ethnology, Bulletin 90.*
By Frances Densmore.
U. S. Government Printing Office
$1.25 *Washington*
5⅝ x 9; xx + 229

A record of the songs of a desert tribe of Indians living in Sonora, Mexico, and southern Arizona, and a description of the ceremonies in which these songs are used.

FAMILIENKUNDE. *Ihre Bedeutung und ihre Ziele.*
By Wilhelm Hussong. *Philipp Reclam*
1.20 marks 3¾ x 6; 144 *Leipzig*

An interesting little contribution to human biology, of especial interest to eugenists and social workers, since it reviews the whole subject of family study. There are 122 citations of literature.

THE GROWTH OF THE WORLD AND OF ITS INHABITANTS.
By H. H. Swinnerton.
Constable and Co., Ltd.
5 shillings 4¾ x 7¼; 211 *London*

This little book will be useful as collateral reading for beginners in natural science courses.

ZOOLOGY

ANTS AND THEIR RELATION TO APHIDS. *Bulletin 341.*
By Charles R. Jones.
Colorado Experiment Station
Free *Fort Collins*
6 x 9; 96 (paper)

Some of the results of this investigation are as follows:

The relation between the ants of the *Formica* group and the aphids of the genus *Aphis* is a good example of mutualism. The ants of the genera *Lasius* and

Formica obtain a larger portion of their food from aphids than do the ants of other genera. The dissemination of aphids by ants is for the purpose of obtaining a greater production of honey-dew, this being accomplished when ants place the aphids on new tender growth where there is an abundance of sap. Aphids in their association with ants are very instrumental in transmitting plant diseases such as cucurbit wilt, fire blight and mosaic disease of sugar cane. An excess of honey-dew on the leaves of plants near large aphid colonies signifies a lack of sufficient ant attendants and is detrimental to the plant.

Included in the text are lists of Colorado ants and records of aphids attended; Colorado ants with the number of genera and species of aphids they attended; aphids with ant attendant; Aphid list with number of genera and species of ant attendants; ants associating together in aphid colonies; and mixed ants with genera and species associating together in aphid colonies. There is an extensive bibliography.

THE INDIAN ZOOLOGICAL MEMOIRS ON INDIAN ANIMAL TYPES. II. SCOLIODON (THE COMMON SHARK OF THE INDIAN SEAS).
By E. Muthammah Thillayampalam.
Lucknow University
2.8 rupees *Lucknow, India*
$6\frac{1}{4}$ x $9\frac{1}{2}$; xi + 116

There being no zoological text-books dealing especially with Indian types available, Indian universities and colleges have been obliged up to the present time, to use English books and laboratory manuals in their zoological courses. These, dealing with types mostly foreign, or at least not common, to India and Indian waters, require importation of specimens from great distances for laboratory use. In order to provide a means for studying the zoological types common to India, a series of monographs is being prepared. The present volume, belonging to this group, substitutes *Scoliodon* (formerly known as *Carcharias*) the common shark of Indian waters, for *Scyllium* of European fame. The work includes sections on classification of Chondrichthyes, bionomics and distribution, external and internal characteristics, development, directions for laboratory work and a bibliography of 160 titles.

THE AVIFAUNA OF EMERYVILLE SHELLMOUND.
By Hildegarde Howard.
University of California Press
$1.25 *Berkeley*
7 x $10\frac{5}{8}$; 86 + 4 plates (paper)

Out of something over 6700 bird bones collected from the mound, 4155 are identifiable. These represent 50 species of birds, of which 45 are found today in the San Francisco Bay region. The bones are in an excellent state of preservation. Usually the limb bones are broken into two or three pieces. This breakage probably occurred before the bones were thrown into the mound, many of them being charred at the broken ends. The age of the Emeryville mound is uncertain, but there seems to be no doubt that the latest date of occupation was prehistoric. From a study of the bird bones the author deduces a number of interesting facts concerning the habits of the Indians who inhabited this region while the mound was being formed. The book contains tables of bone measurements, and a table giving a comparison of the avifauna of Emeryville shell mound with recent and Pleistocene avifaunas.

THE FISHES OF OCEANIA. *Memoirs of the Bernice P. Bishop Museum. Volume X.*
By Henry W. Fowler.

Bernice P. Bishop Museum
$8.00 *Honolulu*
9½ x 12½; iii + 540 (paper)

Oceania comprises that extensive area in the tropical Pacific region, within which lie four principal faunal divisions: Melanesia, including New Guinea and Waigin; Micronesia; Polynesia, including Fiji; and Hawaii. The author of this memoir considers that he has herein described probably not more than half the species inhabiting these waters. Even so, an enormous amount of labor and care went into its preparation, as the large number of species listed and the detailed descriptions testify. The volume is issued in the same handsome form which characterizes all of the memoirs issued by the Bernice P. Bishop Museum of Honolulu. The plates, in monotone, convey a very definite idea of the distinguishing features of the specimens illustrated, if not of the brilliant coloring. There is an excellent index.

DIE RÄTSEL DES VOGELZUGES. *Ihre Lösung aus experimentellem Wege durch Luftfahrt und Vogelberingung.*
By Friedrich von Lucanus.
Hermann Beyer und Söhne
8.40 marks *Langensalza*
6¼ x 9½; x + 266 (paper)

The third edition of a well known and extremely interesting treatise on bird migration, considered especially in its biological aspects. This edition brings the review of the literature up to date, and discusses the latest results from the bird banding experiments in various parts of the world. The author points out that there are now available data on the results of bird banding for 170 different species.

EINLEITUNG IN DIE PHYSIOLOGISCHE ZOOLOGIE (*Physikalische und Chemische Funktionen des Tierkörpers*).
By Hans Przibram. *Franz Deuticke*
10 marks *Leipzig und Wien*
6¼ x 9½; vi + 182 (paper)

A condensed digest of the literature of physiological zoology, using the term in the sense of chemical and physical aspects of animal function. The author expresses the hope that this book may serve the same function that his corresponding well known treatise has in the field of experimental morphology. The book is well indexed. In lieu of a detailed bibliography the author refers to a few well known large handbooks with full bibliographies.

INVESTIGATION OF THE PHYSICAL CONDITIONS CONTROLLING SPAWNING OF OYSTERS AND THE OCCURRENCE, DISTRIBUTION, AND SETTING OF OYSTER LARVAE IN MILFORD HARBOR, CONNECTICUT. *Bureau of Fisheries Document No. 1054.*
By Herbert F. Prytherch.
U. S. Government Printing Office
25 cents *Washington*
7⅜ x 11; 74 (paper)

The investigation here reported was directed to the elucidation of the physical conditions that affect oyster production in inshore waters. Included as factors studied are temperature, tide, salinity, hydrogen-ion concentration, and river discharge, and also biological observations on the condition of the gonads, time of spawning, occurrence and distribution of larvae and setting. A categorical summary and a bibliography are appended.

DIE TIERWELT DER NORD- UND OSTSEE. *Lieferung XV.*
Edited by G. Grimpe and E. Wagler

Akademische Verlagsgesellschaft m. b. H.
8.80 marks *Leipzig*
6 x 8½; 108 (paper)

A taxonomic and briefly descriptive account of the following classes: *Aculifera* (Nierstrasz and Hoffmann), *Thalassobionte und thalassophile Myriapoda* (Schubart) and *Pisces*. It is part of a series intended as a comprehensive survey of the fauna of the North and Baltic Seas, a number of which have been previously noted in these columns.

DAS LEBEN DER SCHMETTERLINGE.
By Friedrich Schnack. *Jakob Hegner*
7.50 marks (paper) *Hellerau*
10.80 marks (bound)
5¼ x 8¾; 286

In America the popularity of the literary naturalist has declined since the days of John Burroughs; in Germany, apparently, he still flourishes. In this delightful book a novelist and poet, who is also an amateur of butterflies, tells us about some of the species and his adventures with them. The book is beautifully printed; our only wonder is that Herr Schnack did not use to illustrate it the skill in the painting of butterflies which he learned from the *Würzburger Glasermeister*.

HUMAN HELMINTHOLOGY. *A Manual for Clinicians, Sanitarians and Medical Zoologists.*
By E. C. Faust. *Lea and Febiger*
$8.00 *Philadelphia*
5¾ x 9⅛; xxii + 616

An extensive discussion of the science of helminthology by one who has been for many years a teacher and investigator in this field. Much information is presented which has not been hitherto easily available. The book contains numerous excellent illustrations and is well documented and indexed.

PRINCIPLES OF ANIMAL BIOLOGY.
By A. Franklin Shull, with the collaboration of George R. Larue and Alexander R. Ruthven.
McGraw-Hill Book Co., Inc.
$3.50 5⅞ x 9; xiv + 405 *New York*

A third edition, in which the chief changes from the former ones consist in an improvement of the chapter on genetics and of the portion devoted to the morphology and physiology of the higher types. We might ask, out of congenital captiousness, why exactly the same portrait of Gregor Mendel has to be reproduced twice, once on page 23 and again on page 226.

ALLGEMEINE VERGLEICHENDE PHYSIOLOGIE DER TIERE.
By H. J. Jordan.
Walter de Gruyter und Co.
32 marks (paper) *Berlin*
34 marks (bound)
6⅜ x 9½; xxvii + 761

An excellent treatise on the comparative physiology of animals which will be welcomed by all zoologists as a reference work. The standpoint is that of modern general physiology. The arrangement of the material is by a functional classification rather than taxonomic.

FRÜHFORMEN DER GEMEINSCHAFT IN DER TIERWELT.
By Friedrich Hempelmann.
Junker und Dünnhaupt Verlag
1.30 marks 6½ x 9½; 23 (paper) *Berlin*

This is a reprint of a lecture on animal societies which formed one of a series on

social organization. It is an interesting popular summary of well known data from the literature of zoology.

PROPAGATION OF PONDFISHES.
Bureau of Fisheries Document No. 1056.
By M. C. James.
U. S. Government Printing Office
10 cents *Washington*
5¾ x 9⅛; 32 (paper)

The purpose of this report is to present briefly, essential facts related to the purpose of the rearing of pond fishes. It covers the propagation of basses, sunfish and catfish, and takes up questions of site, water, foods, etc., as well as relevant biological characters of the fish.

THE VENUS. *A Quarterly Journal Devoted to the Study of Mollusca.*
Published by The Malacological Society of Japan.
Tokubei Kuroda, Geological Institute, Science College, Kyoto Imperial University, Kyoto, Japan.
Subscription $1.00 (Yen 2.20) per year, post-paid. 6 x 8¾.

BOTANY

THE PLANT-LIFE OF THE BALKAN PENINSULA. *A Phytogeographical Study.*
By W. B. Turrill. *Oxford University Press*
$10.00 (U. S. A.) *New York and London*
30 shillings net 6½ x 9¾; xxiii + 490

An important contribution to studies in geobotany. The author has been singularly fortunate in the region which he selected for his investigation. In the Balkan Peninsula, which for a long geological period was either a part of Asia or a broad isthmus connecting the Asiatic and European continents, there exists a unique flora. Within its boundaries are found plants which have drifted in from both the Asiatic and European regions; the altitude zones furnish a wide range in climatic conditions suitable for the growth of many varieties of plants; there are regions of primitive vegetation, undisturbed by man, similar to the plant covering of much of Europe in pre-glacial times; furthermore, there are many plant species which are indigenous to this region and are to be found nowhere else. Only the seed-bearing plants were studied, the investigator's aim being "to consider every aspect of the spermatophytic flora and vegetation that could throw light on the composition, origin, relationships, distribution, and successional changes of the plant-covering of the area."

Mr. Turrill has done his work with infinite pains and has produced a book of much interest. Of especial value is the analysis of the relation of the Balkan flora to that of the neighboring regions of Europe, Asia and Africa and the determination of the main lines of plant migration into and out of the Peninsula. Distribution tables of species, photographs of plants and of regions, and maps enhance the usefulness of the book. Unfortunately, lack of space prohibited the inclusion of the extensive list of titles dealing with plant life in the Balkans which the author has compiled. He gives, however, a group of selected references at the end of each chapter.

MICROBIOLOGY.
By B. F. Lutman.
McGraw-Hill Book Co., Inc.
$4.00 5¾ x 9; x + 495 *New York*
An excellent presentation of this subject.

The general plan is to discuss molds, yeasts, and bacteria as a group. The larger part of the book consists of descriptions of typical species. These types have been chosen "because they are common and have biological or practical importance, if possible, or both." When the type method cannot be followed satisfactorily, the author falls back on the plan of presenting common methods and results in general chapters. These he places at the beginning of the book and at the end.

The beginning (general) chapters are the author's solution of textbook work while a class is learning some elementary technic in the laboratory. The final chapters are an attempt to place before both teacher and student some of the theories, problems, difficulties, and controversies that confront the modern microbiologist. It has seemed well for the student to leave the subject not with the smug complacency that it is all neat, pat, and settled, but rather that he is looking out over a sea of boiling controversy and that many theories that he has been using may be discarded in another generation.

The book contains many excellent illustrations. Reference lists, frequently lengthy, conclude the different chapters. There is a detailed index.

A TEXTBOOK OF BOTANY.
By J. M. Lowson (Revised in collaboration with the Author by L. C. Fox).
University Tutorial Press, Ltd.
9 s. 6 d. *London*
$4\frac{3}{4}$ x $7\frac{1}{4}$; viii + 656

A seventh edition of a book which has been widely used in English institutions as a general introduction to the study of biology. Prepared to meet the requirements of a wide range of students, it deals in considerable detail with the various branches of the subject. Incorporated in the chapters on "Nutrition and growth" and the "Plant and its enviroment" is a series of 76 experiments for class work. The work concludes with a section containing 152 test questions, an appendix in which many practical suggestions are given and an extensive index. In this edition, numerous changes have been made: obsolete technical terms have been deleted, the subject matter expanded, *Sphaerotheca* added as a type and the number of illustrations increased.

BOTANY. *Principles and Problems.*
By Edmund W. Sinnott.
McGraw-Hill Book Co., Inc.
$3.00 $5\frac{3}{4}$ x 9; xxi + 441 *New York*

A second revised edition of a text-book for elementary work in botany, the essential idea of which is to arouse critical curiosity in the student's mind. Each chapter, after dealing briefly and concisely with the more important facts of the subject under discussion, concludes with lists of "Questions for thought and discussion" and "Reference problems." In all there are 747 in the former group and 238 in the latter. In this edition, the text has been largely rewritten, new material and illustrations added and the "Questions" and "Reference problems" revised considerably. Teachers of botany will find this an excellent book to place in the hands of their students.

THE STRENGTH OF NORTH AMERICAN WOODS. *United States Department of Agriculture Miscellaneous Publication No. 46.*
By H. S. Betts.
U. S. Government Printing Office
5 cents *Washington*
$5\frac{3}{4}$ x $9\frac{1}{8}$; 18 (paper)

The larger part of this paper consists of

a table giving the results of tests to determine the strength of various woods. Something over 125 varieties of wood are listed, while the properties of each, actual and comparative, are given under 21 headings. Among the various records may be mentioned weight per cubic foot (green, air dry, kiln dry); specific gravity, oven dry, based on volume when green; shrinkage from green to oven dry condition (in volume, radial, tangential); strength in bending; stiffness; hardness; etc. There are numerous explanatory notes.

MUSHROOMS OF FIELD AND WOOD.
By Margaret McKenny. *The John Day Co.*
$2.00 5 x 7⅜; xxiii + 193 *New York*

A handbook of the more common American mushrooms, illustrated with excellent photographs and with three color plates. There is a short bibliography and an index.

ACTA FORESTALIA FENNICA 33. Containing following articles: *Männyn Juuristo. Morfologinen Tutkimus. (The Root System of Pine (Pinus Silvestris). A Morphological Investigation. Summary in English)*, by Erkki Laitakari; *Die Wurzelforschung in ihrer Beziehung zur Praktischen Forstwirtschaft*, by Erkki Laitakari; *Über Verhältnis der Winterfestigkeit des Roggens zur Dehnbarkeit und Dehnungsfestigkeit seiner Wurzeln. (Summary in English. On the relation between the hibernation of rye and the tensile strength of its roots)*, by P. Kokkonen.
Society of Forestry in Suomi
Helsinki, Finland
6¼ x 9⅝; 425 + 55 plates

ACTA FORESTALIA FENNICA 34. AIMO KAARLO CAJANDER. *50-Vuotisjuhlajulkaisu. Commentationes in Honorem Professoris A. K. Cajander. Quinquagenarii Editae.*
Society of Forestry in Suomi
Helsinki, Finland
6¼ x 9⅝; 1006 + 31 plates

MORPHOLOGY

THE AUTONOMIC NERVOUS SYSTEM.
By Albert Kuntz. *Lea and Febiger*
$7.00 *Philadelphia*
5¾ x 9¼; xii + 576

In this general survey of a subject which is receiving an ever increasing amount of attention by the clinician and the surgeon, the author describes in a thoroughly comprehensive manner what is known to date concerning the autonomic nervous system. After a discussion of the morphology, physiology and development of the autonomic nervous system, he devotes much space to the innervation of the organs of the body. He then takes up pathological conditions. Visceral sensitivity and referred pain he treats in detail as well as the surgery of the autonomic nervous system. A lengthy bibliography (over sixty pages) adds greatly to the usefulness of the book. There is a group of well selected illustrations and an index.

BIOLOGIE DER GELENKE.
By Walther Müller.
Johann Ambrosius Barth
15 marks (paper) *Leipzig*
17 marks (bound)
6¾ x 9⅞; vii + 170

This is a thorough and useful discussion of the anatomy and physiology of joints, growing out of the author's investigations in the field of experimental orthopedics. The subjects treated are: the biology of joint cartilage; the biology of the joints;

arthritis deformans from the viewpoint of joint biology; the biology of the synovia and the joint capsule; the relation of the joints to the muscular, nervous, and endocrine systems; air pressure relations in joint regions. There is a bibliography of 10 pages and an adequate index. An excellent treatise on an interesting subject.

LEHRBUCH DER ENTWICKLUNGSGESCHICHTE. *Fünfte, vollständig neubearbeitete Auflage.*
By Robert Bonnet herausgegeben von Dr. Karl Peter. *Paul Parey*
28 marks *Berlin*
$6\frac{1}{2}$ x $9\frac{1}{2}$; x + 542

This fifth edition of Bonnet's textbook of embryology, which first appeared nearly a quarter of a century ago, has been almost completely rewritten by Dr. Peter, in order to bring it into accord with present day points of view. Its usefulness as an introductory text is thus ensured for another long period. There is appended a useful glossary of technical terms derived from Greek.

PHYSIOLOGY AND PATHOLOGY

THE PHYSIOLOGICAL MECHANICS OF PIANO TECHNIQUE. *An experimental study of the nature of muscular action as used in piano playing, and of the effects thereof upon the piano key and the piano tone. By Otto Ortmann.*
E. P. Dutton and Co., Inc.
$6.50 $5\frac{1}{4}$ x $8\frac{1}{2}$; xv + 395 *New York*

It is a rare thing to find combined in one person thorough training and competence as a professional musician, on the one hand, and equally thorough training and competence as a scientist, on the other hand. This combination is exemplified, and indeed adorned, in the person of the author of this volume. Dr. Ortmann is the Director of the Peabody Conservatory of Music in Baltimore, a Hopkins Ph.D. in psychology, and, withal a scholar and an artist. In an earlier volume he has discussed the physics of piano playing. In the present one he treats of the physiology of that art. A third volume to deal with its psychology is promised. While perhaps merely the expression of a personal prejudice of the present reviewer, it is his opinion, for what it may be worth, that the ultimate valuation and permanent usefulness of this book will be as a contribution to physiology rather than to art. For obvious reasons physiology has, in the main, attempted to study only the simplest muscular movements. Here we have a courageous, and on the whole successful, attempt to analyze scientifically one of the most complicated, delicate, intricate, and highly coordinated and integrated sets of muscular movements that is known. In this attempt Dr. Ortmann has used standard physiological methods of recording, which, while not the most refined now available, are entirely adequate to his purpose. While thorough and painstaking, at times almost to the point of pedantry, the book is nevertheless extremely interesting, at least to the philosophical biologist. It is a fine, critical, intelligent piece of research. How the pianist will regard it we do not know. Probably chiefly as an exhibition book, to adorn the shelf and vicariously prove by its mere unread presence the intellectuality of the owner. Real musicians, bless their hearts, commonly enjoy exercising their fingers more than they do their brains.

PROGRESSIVE RELAXATION. *A Physiological and Clinical Investigation of*

Muscular States and their Significance in Psychology and Medical Practice.
By Edmund Jacobson.
University of Chicago Press
$5.00 6 x 9; xiii + 429 *Chicago*

It is only fairly recently that what is certainly the most important factor, as well as one of the oldest known remedies, in the treatment of a vast number of bodily ills, has received careful, systematic study in the laboratory. The author of this book has devoted much time to an investigation of the purely physiological effects of rest on the human system and herein sums up the results of his work and gives a method for the application of what he terms "progressive relaxation" in the treatment of such cases as involve neuromuscular disorders. In progressive relaxation, suggestion or other psychotherapeutic measures play no part.

It is impossible to mention the many interesting details which this highly important work brings out. Its scope can best be indicated by giving some of the chapter headings: General features of neuromuscular hypertension; general features of progressive relaxation; the technic of progressive relaxation; the nature and technic of differential relaxation; the influence of relaxation upon the reflex reaction to sudden pain (flexion reflex); the influence of relaxation upon the knee-jerk; the influence of relaxation upon mental activities; the therapeutic use of relaxation, etc. In a section on "Explanatory Principles" the author gives some of the salient features of relaxation. Progressive relaxation is cultivated natural relaxation, a purely physiologic occurrence, which brings about a complete release of nervous tension. Learning to relax requires work on the part of the patient. He is instructed by his physician to do certain things in a particular way. He goes through the learning process by the method of trial and error. Once his education is complete the patient can, on his own initiative, apply his skill in many ways towards a more rational way of conserving his nervous energy. Successful relaxation produces a feeling of well-being. It leads also to independence of manner and attitude; the longer the training, the greater on the whole becomes the independence.

This book will be extremely useful to the general practitioner, the surgeon and neurologist. It is well documented and contains author and subject indices.

LE PROBLÈME DES GLANDES À SÉCRÉTION INTERNE. *Les Propriétés physicochimiques et pharmacodynamiques des Hormones. XII. I. L'Hypophyse.*
By H. Penau, L. Blanchard and H. Simonnet.
Les Presses Universitaires de France
45 francs 6 x 9¼; viii + 249 *Paris*

An excellent brief résumé of the present state of knowledge regarding the biological effects of the internal secretions from the two lobes of the pituitary body. The bibliography covers 25 closely printed pages and includes the literature up to January 1, 1928. The citations are not confined to French work, but the significant work which has been done in other countries is carefully reviewed, especially the American. The authors take a sane and conservative position regarding endocrinology generally, and are at pains to point out the silliness of what they call "endocrine fatalism," which would throw away our heredity, our intellectual faculties, our will, and our education. A useful book.

BAINBRIDGE AND MENZIES' ESSENTIALS OF PHYSIOLOGY. *Sixth Edition. Edited and Revised by H. Hartridge.*

Longmans, Green and Co.
$5.00 5⅜ x 8½; xii + 528 *New York*

The primary object of this book was to meet the requirements of the medical student preparing for a pass examination in the subject of Physiology. Matter dealt with in laboratory text-books and all subjects of purely historical interest were excluded, so far as possible. In this edition, the sixth, the author has wrought many changes. New chapters have been written on basic principles, muscles, nerve, the central nervous system, vision, hearing, the liver, exercise and work. New sections have been added on capillary circulation, the vitamins, the kidney, etc. Many new diagrams have been substituted for those formerly used. One of the most useful features of the book is the carefully prepared index.

THE ORIGIN OF MALIGNANT TUMORS.

By Theodor Boveri (translated by Marcella Boveri). *The Williams and Wilkins Co.*
$2.50 5¼ x 8; ix + 119 *Baltimore*

This treatise, by the late Theodor Boveri, appeared originally in Germany in 1914. The author summarizes his work in experimental cytology and discusses the relation which nuclear defects might have to malignant tumors. His conception is that "the cell of a malignant tumor is in some way a defective cell; it has lost some qualities of normal tissue-cells. . . . In this altered condition, the cell reacts differently to its surroundings, and this might be the sole cause of the tendency to unchecked cell multiplication." A "definite abnormal chromosome-complex" can explain certain characteristics of malignant tumors, among which are defective histological form and the altered biochemical behavior of tumor cells. The author suggests many lines of work in this field which those who are studying the cytology of cancer will find interesting and valuable.

CEREBROSPINAL FLUID IN HEALTH AND DISEASE.

By Abraham Levinson. *C. V. Mosby Co.*
$8.00 6 x 9; 386 *St. Louis*

A third edition of a highly useful book. It has been thoroughly revised to include all the recent important contributions on the subject. There has been a rearrangement of chapters so that the clinical sections are separated from the theoretical sections.

ANNALS OF THE PICKETT-THOMSON RESEARCH LABORATORY. Vol. V. *The Pathogenic Streptococci. Their Rôle in Human and Animal Disease (continued).*
The Williams and Wilkins Co.
$10.00 *Baltimore*
8½ x 11; xi + 392 (paper)

BIBLIOGRAPHY ON COD-LIVER OIL IN ANIMAL FEEDING *with Noncritical Comments and Abstracts. Bureau of Fisheries Document No. 1065.*
By John R. Manning.
U. S. Government Printing Office
10 cents *Washington*
6 x 9¼; 33 (paper)

BIOCHEMISTRY

MECHANISM OF ENZYME ACTION AND ASSOCIATED CELL PHENOMENA.

By F. F. Nord.
The Williams and Wilkins Co.

$2.00 5¾ x 9; ix + 78 *Baltimore*

This little book was written for the purpose of furnishing the student with a survey of certain phases of enzyme chemistry as a preliminary preparation for more detailed work in a highly complicated field. The author has succeeded admirably in giving a clear, concise presentation of the subject. He includes a bibliography of 189 titles. There is no index.

SEX

STERILIZATION FOR HUMAN BETTERMENT. *A Summary of Results of 6,000 Operations in California, 1909-1929.* *By E. S. Gosney and Paul Popenoe.* *The Macmillan Co.*

$2.00 5 x 7⅜; xviii + 202 *New York*

In this book is summarized the work which has been done prior to January 1, 1929, on the sterilization of defectives in California state hospitals. Much of the material included in this report has appeared at various times in technical journals. In all 6,255 individuals have been sterilized, a far larger number than have been so treated in any other single state where there are laws permitting sterilization. In fact, it is three times the total for all such states. The first part of the book gives a survey of the results of the sterilizations in the state hospitals, so far as it has been possible to follow up the individuals. The second part deals with general conclusions based on these studies and a consideration of the results of sterilization operations elsewhere. In the appendix there are nine chapters which deal with various phases of the subject, among which may be mentioned a list of technical papers on eugenic sterilization in California, an article on medical aspects of sterilization, by Dr. Robert L. Dickinson of New York, and an outline of a state law providing for sterilization. Reginald, the Office Boy, says that the most important thing in the book—and perhaps he is right—is the statement that sterilization "has no effect upon sex desire, sex performance, or sex feeling of the subject, except a favorable psychological effect in some cases, particularly where the fear of pregnancy is removed." But what of their prostates in the long run?

FACTORS IN THE SEX LIFE OF TWENTY-TWO HUNDRED WOMEN. *By Katharine Bement Davis. Harper and Bros.*

$3.50 6 x 9¼; xx + 430 *New York*

Realizing the need for more knowledge of the sex life of the normal individual, the Secretary of the Bureau of Social Hygiene here analyses the results of questionnaires obtained from 1000 married women and 1200 single women. The following subjects are treated: the use of contraceptives; frequency of intercourse as a possible factor in sterility; the happiness of married life; some auto-erotic practices; the periodicity of sex desire; homosexuality. We note from the table on "Sources of information as to contraceptive measures" that two women obtained their information from the Bible. This raises the interesting question whether it is not the duty of our customs authorities to exclude the Bible from this country, along with the works of Marie C. Stopes.

REPORT ON PHYSICIANS' REPLIES TO QUESTIONNAIRE CONCERNING THEIR EXPERIENCE WITH THE VAGINAL DIAPHRAGM AND JELLY. *Prepared by the Research Department of Holland-Rantos Co., Inc.*

Sent on request. *New York*

6 x 9; 27 (paper)

A high-toned piece of salesmanship, evidencing the progress of the world, on the one hand, and the need for further physiological research towards a perfect contraceptive, on the other hand.

A STUDY OF MASTURBATION AND THE PSYCHOSEXUAL LIFE.
By John F. W. Meagher.
William Wood and Co.
$2.00 5 x 7¾; 130 *New York*

It is an encouraging sign that this temperately written book on a subject about which so much is popularly known "that ain't so" should reach a second edition. Dr. Meagher concludes that "the harm resulting from excessive indulgence in the habit is chiefly in the mental and moral spheres, rather than in the physical sphere." There are author and subject indexes.

THE PHYSIOLOGY OF LOVE.
By George M. Katsainos. *The author*
$4.00 *176 Huntington Ave., Boston*
6 x 9⅛; 326

The author, who appears to have hitherto written chiefly about syphilis, begins with the incontrovertible statement that "Man is a singular creature." The same remark may be made with equal justice about this book. It is an amazing *mélange* of autobiography, sexology, subtle eroticism, anti-feminism, metaphysics, and—so Reginald the Office Boy (who *will* surreptitiously read books which no pure young man should) says—blah. At the same time a cynical Pantagruelist will get an hour's amusement out of running through the book.

BIOMETRY

THE ADJUSTMENT OF ERRORS IN PRACTICAL SCIENCE.
By R. W. M. Gibbs. *Oxford University Press*
$1.75 4¾ x 7 ; 112 *New York*

An excellent presentation of the theory of errors, simply and clearly written, and covering the normal curve of errors, area and volume distributions of errors, the method of least squares, the correlation coefficient, partial correlation, the correlation ratios, etc. The more mathematical portions have been isolated in an appendix, where there is no danger of their frightening the non-mathematical student.

FORTUNA *or Chance and Design.*
By Norwood Young.
E. P. Dutton and Co., Inc.
$1.00 4⅛ x 6; 93 *New York*

An entertaining account of roulette, horse racing and other devices for losing money easily and rapidly.

PSYCHOLOGY AND BEHAVIOR

FEELINGS AND EMOTIONS. *The Wittenberg Symposium.*
By Thirty-four Psychologists, edited by Martin L. Reymert. *Clark University Press*
$6.00 6 x 9; 454 *Worcester*

In this book are printed the papers given by various eminent psychologists at the symposium held on the occasion of the inauguration of the new Psychological Laboratory of Wittenberg College, Springfield, Ohio. Dr. Cattell, a competent judge, doubts "whether there has ever been held a meeting of psychologists in which were presented so many papers of such high average merit." The papers of the symposium are as follows: Is "emo-

tion" more than a chapter heading? by Madison Bentley; The place of emotion in modern psychology, by Joseph Jastrow; A new method for investigating the springs of action, by Charles E. Spearman; Emotion, conation, and will, by F. Aveling; The essence of feeling: outline of a systematic theory, by F. Krueger; The feeling-tone of sensation, by F. Kiesow; Emotion and thought: a motor theory of their relations, by Margaret F. Washburn; The utility of emotions, by W. B. Pillsbury; Feelings and emotions, by Ed. Claparède; A functional theory of the emotions, by D. T. Howard; Emotion as a dynamic background, by Knight Dunlap; Can emotion be regarded as energy? by Morton Prince; Feeling and emotion as forms of behavior, by Albert P. Weiss; Displeasure and pleasure in relation to activity, by Karl Bühler; Emotion and feeling distinguished, by William McDougall; Phonophotography as a new approach to the psychology of emotion, by Carl E. Seashore; Excitement as an undifferentiated emotion, by George M. Stratton; How emotions are identified and classified, by Robert S. Woodworth; The differentia of an emotion, by Harvey A. Carr; Pleasantness and unpleasantness as modes of bodily experience, by L. B. Hoisington; Pleasurable reactions to tactual stimuli, by Robert H. Gault; Neural organization for emotional expression, by Walter B. Cannon; Emotions as somato-mimetic reflexes, by Vladimir M. Bekhterev; Emotion in animals and man, by Henri Piéron; Fear of action as an essential element in the sentiment of melancholia, by Pierre Janet; A theory of elements in the emotions, by Carl Jörgensen; Feelings and emotions from the standpoint of individual psychology, by Alfred Adler; "Ernstspiel" and the affective life: a contribution to the psychology of personality, by Wilhelm Stern; The development of conscience in the child as revealed by his talks with adults, by David Katz; The rôle of feeling and emotion in aesthetics, by Herbert S. Langfeld; Psychological and psychophysical investigations of types in their relation to the psychology of religion, by Erich Jaensch; Feelings and emotions in the psychology of religion, by D. Werner Gruehn; Historical development of the theory of emotions, by G. S. Brett; Training the emotions, by John S. Terry.

AN INTRODUCTION TO THE STUDY OF BIRD BEHAVIOR.
By H. Eliot Howard.

Cambridge University Press
£2, 2s. 9¾ x 12½; xii + 136 *London*
$14.00 *The Macmillan Company*
New York

Mr. H. Eliot Howard is well known from his earlier studies in bird behavior. The present volume will substantially add to his reputation. It embodies a thorough-going observational and experimental study of the breeding behavior of, first, a reed-bunting, *Emberiza schoeniclus schoeniclus*, and, second, a yellow-bunting, *Emberiza citrinella citrinella*. The record of the observational work in the field bears in every line the marks of unhurried thoroughness, precision, exactness, penetration and understanding. The two observational chapters are followed by longer chapters analyzing the behavior into its components. The two final chapters attempt a synthesis under the attractive headings "The Whole Has Value, the Parts by Themselves have None," and "An Approach to a Mind Story." The general conclusion reached is against the behaviorist position of Watson and in favor of cognitive reference and revival in the form of imagery. The book is beautifully printed and illustrated, and is a contribution to animal psychology of first-rate importance.

REASONING IN WHITE RATS.
By Norman R. F. Maier.
The Johns Hopkins Press
$1.75 7 x 10½; 93 (paper) *Baltimore*

Lack of space permits only a few of the results of this interesting series of experiments on reasoning in rats to be given. The author found that:

> Rats can combine the essential relations of one situation with those of another in such a way as to reach the goal which could not be reached by any one concrete experience. They can adequately adjust themselves to a new situation without "trial and error," but with intelligence and insight.
>
> The behavior of a rat varies for the same situation. The end determines the response and the means to the end may vary.
>
> A rat can select the shorter of several routes to food in a known situation without first going over them in connection with food or in any special and invariable order.
>
> The knowledge of a situation is spatial and not a series of successive experiences for the rat. When the rat is familiar with a situation, it knows it as an immediate whole.

A STUDY OF THE RELATIONSHIP BETWEEN THE INTELLIGENCE AND MORAL JUDGMENTS OF COLLEGE STUDENTS. *Peabody Contributions to Education No. 51.*
By Paul L. Boynton.
George Peabody College for Teachers
75 cents 6 x 9; 49 (paper) *Nashville*

The subjects were 243 students, 120 girls and 123 boys. The criteria of intelligence were Army Alpha scores or other tests translated into these. The criteria of moral judgment consisted of scores set down by the subjects as to the moral heinousness of lapses in such matters as Sunday observance, taking life, use of stimulants, etc.; when no wrong was considered involved a mark of 0 was assigned, when an act was as wrong as could be, a mark of 10. Thus a low score indicated moral leniency, a high score moral stringency. The outstanding characteristics of the results is that there is a lack of relation between intelligence and moral judgment, although there does appear to be a weak tendency for high intelligence to be accompanied by relatively lenient judgment.

THE THINKING MACHINE.
By C. Judson Herrick.
The University of Chicago Press
$3.00 5 x 7⅞; xii + 374 *Chicago*

A clear and interesting account for the general reader of neurology, and of psychology from a neurological standpoint. The trouble with most mechanistic treatments of biology and psychology, Dr. Herrick finds, is that they do not take a wide enough view of the nature of a machine. By enlarging the conception of a machine to include everything that performs work by natural agencies in accordance with natural laws, he finds that all life, including the mental or spiritual life, is a mechanistic process and can be explored by the scientific method.

DIE PSYCHISCHEN REAKTIONSFORMEN.
By Harry Marcuse. *S. Karger*
22 marks 7 x 10¼; 262 *Berlin*

This is an attempt to demonstrate the practical application of Jasper's "energetic theory of psychoses" by examples drawn from the clinic and the laboratory. The treatment is broadly biological, and the book will interest psychologists and students of behavior generally. Its usefulness is diminished by the lack of an index.

THE COMMON SENSE OF DREAMS.
By Henry J. Watt. *Clark University Press*
$3.00 6 x 9; xvii + 212 *Worcester*

A Scotch psychologist, who thinks there is something in psychoanalysis but is repelled by the vagueness and mysticism of its technique, develops in this book a simpler and less fantastic scheme for the interpretation of dreams.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

THE SCOTS KITCHEN. *Its Traditions and Lore with Old-Time Recipes.*
By F. Marian McNeill.
Blackie and Son (Canada), Ltd.
$2.25 5¼ x 7¾; xvi + 259 *Toronto*

This delightful book gives not only a great many old Scottish recipes (something over 260 in all) but includes much that is interesting pertaining to the history of Scottish social life. If any one supposes that the Scots of old lived solely on the coarser varieties of food, he has only to glance through this book to be otherwise convinced. Numerous recipes are most alluring As a random sample we give the following: Partan Bree (crab soup), Lobster-Haut Goût, Roast Grouse, Haggis Royal, Scots Apple Pudding, Whim-Wham, and Scots Woodcock. Kings and noblemen, especially during Edinburgh's golden age, had French cooks, and they undoubtedly influenced Scottish cuisine to a considerable extent. Many of the fine old recipes, however, originated in the cottage kitchen. In the appendix there are sections on Franco-Scottish domestic terms, old Scottish measures, old Scottish festival cakes and dishes, and sources of recipes. There is an index of recipes.

SCIENCE AND THOUGHT IN THE FIFTEENTH CENTURY. *Studies in the History of Medicine and Surgery, Natural and Mathematical Science, Philosophy and Politics.*
By Lynn Thorndike.
Columbia University Press
$4.75 5⅞ x 9; xii + 387 *New York*

Probably no period in the history of civilization is so bound in summary generalities as the Middle Ages, of which it has been said that they are called dark because we know so little about them. The monumental researches of this author as exemplified in his *History of Magic and Experimental Science* and this volume will go far to establish a more authentic view of those formative centuries than we now have. Contrast the glib assurances of our text books with the caution of the scholar; "It is hardly possible as yet to draw a general picture of fifteenth century thought and science." Like the earlier work mentioned this is no comprehensive history, but rather a source book to which future general historians will turn for enlightenment. It consists of special studies in the science and thought of the fifteenth century based on manuscript and unpublished materials. A great learning went into its making and a great industry.

MYSTICISM AND LOGIC.
By Bertrand Russell.
W. W. Norton and Co., Inc.
$3.00 5½ x 8½; 234 *New York*

Another volume in the popular priced reeditions of Russell's works which are being issued from this press. It contains some of the philosopher's most readable and oft-quoted essays. "Mathematics and the metaphysicians" is there and so is "A Free Man's Worship." In a new introduction which the author prepared

for this edition he declares certain changes from the philosophic position taken when the work was first written some fifteen years ago. One gathers from his remarks that Mr. Russell is now a good deal of a pragmatist.

A HANDBOOK ON HANGING. *Being a short Introduction to the fine art of Execution, and containing much useful information on Neck-Breaking, Throttling, Strangling, Asphyxiation, Decapitation and Electrocution; as well as Data and Wrinkles for Hangmen, an account of the late Mr. Berry's method of Killing and his working list of Drops; to which is added a Hangman's Ready Reckoner and certain other items of interest. All very proper to be read and kept in every family.*

By Charles Duff. Hale, Cushman and Flint $1.50 4 x 6⅝; 130 *Boston*

A satire directed against capital punishment. It takes the form of a defense of the hangman as an artist worthy of more attention and respect than he now gets. It is only mildly amusing in its humorous portions and where it is meant to horrify, is too refined, we are afraid, to shock a public hardened as we are by tales of the late war.